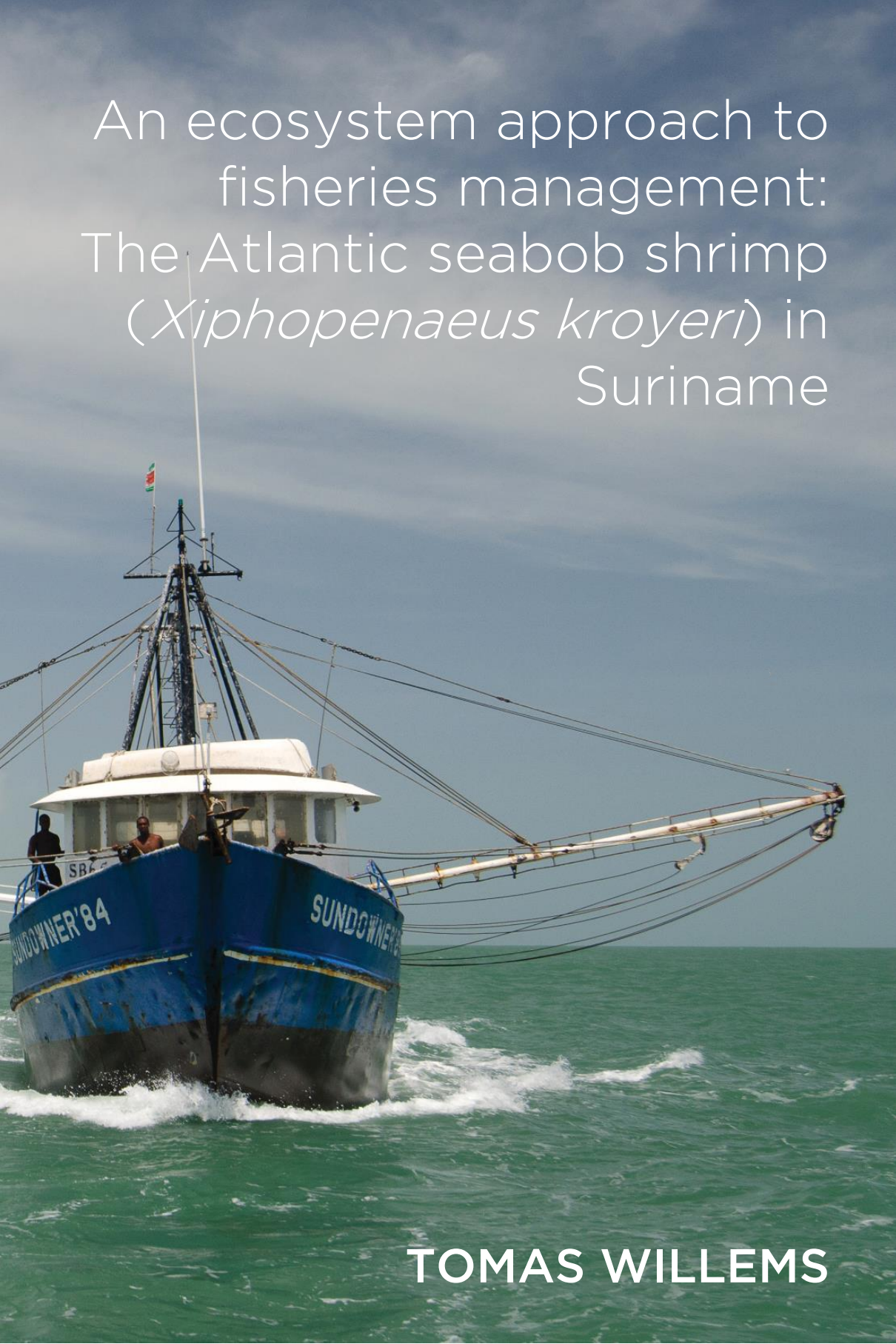
An ecosystem approach to fisheries management: The Atlantic seabob shrimp (*Xiphopenaeus kroyeri*) in Suriname



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AN ECOSYSTEM APPROACH TO FISHERIES MANAGEMENT: THE ATLANTIC SEABOB SHRIMP *(XIPHOPENAEUS KROYERI)* IN SURINAME

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AN ECOSYSTEM APPROACH TO FISHERIES MANAGEMENT: THE ATLANTIC SEABOB SHRIMP *(XIPHOPENAEUS KROYERI)* IN SURINAME

EEN ECOSYSTEEMBENADERING IN VISSERIJBEHEER: DE ATLANTISCHE SEABOBGARNAAL *(XIPHOPENAEUS KROYERI)* IN SURINAME

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TABLE OF CONTENTS

SUMMARY

The Ecosystem Approach to Fisheries (EAF) is widely acknowledged as being the best approach to future fisheries management. In contrast to traditional single-species management, an EAF explicitly recognizes the complexity of ecosystems in which fisheries operate. As such, fundamental elements to be considered in an EAF include: (1) the trophic relationships between exploited species and their food sources, (2) indirect interactions between fishing fleets - through trophic linkages or bycatch - and (3) the impact of fishing on marine habitats and species communities. The disregard of these aspects in fisheries management lies at the basis of several environmental and socio-economic problems associated with tropical shrimp trawl fisheries. These fisheries remain the main supplier of shrimp to the global market, but face a negative public perception. The increasing market demand for sustainable seafood products has triggered the fishery for Atlantic seabob shrimp *Xiphopenaeus kroyeri* (Crustacea: Penaeoidea) off the coast of Suriname to take steps towards more environmentally sustainable fishing practices. This led to the seabob fishery obtaining a Marine Stewardship Council (MSC) ecolabel in 2011, which is already a major step towards the implementation of an EAF. Nevertheless, as highlighted during the MSC assessments, crucial information is lacking to assess the impact of seabob fisheries on certain aspects of the regional ecosystem structure and functioning. **This doctoral thesis aimed to provide relevant knowledge needed for an improved ecosystem approach to the management of *Xiphopenaeus kroyeri* trawl fisheries off Suriname. More specifically, we focused on (1) the characterization of the benthic assemblages and habitats of the inner continental shelf where *X. kroyeri* fisheries take place (ecosystem structure), (2) the role of *X. kroyeri* in the coastal food web of Suriname (ecosystem functioning), (3) the impact of *X. kroyeri* trawling on ecosystem structure and functioning (ecosystem impact) and (4) the translation of the scientific results into recommendations for fisheries management (management implications).**

Chapter 1 sets the broader scene by introducing the current fisheries crisis, the EAF concept and the MSC ecolabel. Next, the problems and challenges related to shrimp fisheries and more specifically to seabob fisheries in Suriname are outlined. The thesis further constitutes of seven chapters which are organized in four parts, each related to one of the four objectives of this doctoral study.

Since ecological research on the Suriname continental shelf has been limited, **Chapters 2 and 3** (i.e. **PART I**) aimed to characterize the **demersal assemblages in the coastal waters of Suriname**. Therefore, epibenthos, demersal fish and environmental parameters were sampled during an extensive trawl survey in 2012-2013. Data were collected on a (bi)monthly basis at 15 locations in the shallow (<40 m) coastal area. The spatio-temporal distribution of epibenthic

fauna was described in **Chapter 2**, together with the abiotic characteristics of the inner Suriname Shelf. From 148 trawl samples, 92 epibentic taxa were identified. These occurred in three spatially distinct species assemblages, related to clear gradients in some environmental parameters. A species-poor *coastal* assemblage, dominated by *X. kroyeri,* was discerned within the muddy, turbid-water zone (6 to 20 m depth). Close to the 30 m isobath, sediments were much coarser (median grain size on average 345 ± 103 μm vs. 128 ± 53 μm in the *coastal* assemblage) and water transparency was much higher (on average 7.6 ± 3.5 m vs. 2.4 ± 2.1 m in the *coastal* assemblage). In this zone, a diverse *offshore* epibenthic assemblage was found, characterized by brittle stars (mainly *Ophioderma brevispina* and *Ophiolepis elegans*) and a variety of crabs, sea stars and hermit crabs. A *transition* assemblage occurred in between both zones, with epibenthic species typically found in either the *coastal* or *offshore* assemblages, but mainly characterized by the absence of *X. kroyeri*.

The demersal fish community of the inner Suriname Shelf **(Chapter 3)** included 98 species, but trawl samples were dominated by *Stellifer rastrifer, Amphiarius rugispinis* and *Cynoscion jamaicensis,* which accounted for 50 % of the catches by number. In analogy with the epibenthic community, cluster analysis revealed three species assemblages in a nearshore-offshore depth gradient. The *coastal* fish assemblage, occurring in the shallow turbid waters up to 20 m depth, represented the 'sciaenid community' of tropical shelves and was dominated by Sciaenidae and Ariidae. Around 27 m water depth, a *transition* assemblage marked the shift towards a very different *offshore* fish assemblage on the deepest sampling locations (34 m). The *offshore* assemblage had a significantly lower demersal fish density and diversity, and contained representatives of fish families typical for deeper tropical shelves, such as Paralichthyidae, Triglidae and Lutjanidae. Although clear seasonal differences were noted in the environmental characteristics (e.g. dry vs. rainy season), little temporal variation was observed in the communities of epibenthos and demersal fish. They were primarily spatially structured, in an on-offshore gradient related to depth, sediment grain size and sediment total organic carbon content. The shift between the *coastal* and *offshore* assemblages was the most important feature of the benthic communities of the inner Suriname Shelf, and coincided with a transition between two principal ecosystems: a coastal, river influenced system fueled by detritus versus an open shelf system based on primary production. Demersal fishes thrived in the coastal ecosystem, together with a potentially important epibenthic food source, the seabob shrimp *X. kroyeri,* which reached very high densities (up to 1383 individuals 1000 m^{-2}). Further, the shallow nearshore waters at less than 20 m depth may have an important nursery function, because juveniles of commercially important demersal fishes were abundant in our *coastal* trawl catches.

The first part of the thesis made clear that *X. kroyeri* dominates the epibenthic community of the coastal waters (<27 m depth) off Suriname, and that its

occurrence coincides with a diverse demersal fish assemblage. In **PART II, the role of *X. kroyeri* in the coastal food web of Suriname** was assessed, by identifying its prey and predators. **Chapter 4** investigated the trophic ecology of *X. kroyeri* by using a combination of stomach content analyses and dual stable isotope analyses. It appeared that this coastal penaeid shrimp species has a rather omnivorous diet, feeding opportunistically on both animal prey and primary food sources. Judging from their depleted ^{13}C values, coastal sedimentary and suspended organic matter, and carbon from riverine and mangrove-derived detritus were not incorporated by *X. kroyeri*. An ontogenetic diet shift was observed from postlavae to juveniles and adults. Adult *X. kroyeri* were located higher in the food chain, mainly preying on larger benthic organisms like hyperbenthic crustaceans. These included copepods, amphipods and the luciferid shrimp *Lucifer faxoni*, which are mainly preyed upon during daytime when these prey typically reside near the seabed. Benthic microalgae (BM) from intertidal mudflats and offshore sedimentary organic matter were important primary food sources for all life stages of *X. kroyeri*. Intertidal BM contributed up to 64 % to the overall diet based on a Bayesian mixing model. Our results indicated that primary production on intertidal mudflats, through BM, forms an important energy source for the subtidal turbid-water food web.

The next step in studying the functional role of *X. kroyeri* was to assess whether it is an important prey for higher trophic levels. This was tackled in **Chapter 5**, which evaluated the trophic importance of *X. kroyeri* for the demersal fish community on the inner continental shelf of Suriname. The diet of 13 common fish species was investigated by means of stomach content and stable carbon/nitrogen isotope analyses. Atlantic seabob shrimps occurred in the stomachs of 11 fish species, and the isotopic niche of the demersal fish community considerably overlapped with the theoretical isotopic niche of a *X. kroyeri* predator. Two trophic guilds could be discerned: epi-piscivores and benthivores. The first group were mainly Sciaenidae, and fed on a mixture of fish and shrimp, with gravimetrical diet contributions of *X. kroyeri* around 40 %. The epi-piscivores also included one fish specialist (*Gymnura micrura*) and two shrimp specialists (*Nebris microps* and *Cynoscion virescens*). The benthivore feeding guild was taxonomically more diverse and showed a more diverse diet. Their stomachs contained significant proportions of 'digested debris', partly originating from *X. kroyeri*. The results showed that a significant amount of energy in the benthic food web of the inner Suriname Shelf is channeled in a 'wasp-waist' pattern at the intermediate trophic level, through the abundant and productive benthic invertebrate *X. kroyeri*.

Whereas the first two parts of the thesis studied aspects of ecosystem structure and functioning, **PART III** aimed to assess **the impact of *X. kroyeri* trawl fisheries on the coastal ecosystem of Suriname.** The impact on demersal assemblages was the main focus of **Chapter 6**, which investigated the catch composition of seabob trawl fisheries off Suriname. This was done by analyzing

68 catch samples, taken both during day and night on six commercial fishing trips between April and November 2014. Catch rate in the seabob fishery averaged 205 3 180 kg of total catch per hour of trawling. Catches were dominated by seabob shrimp, accounting for 59 ± 13 % of the total catch by weight. The bycatch was dominated by fish (31 ± 14 % of total catch), followed by jellyfish (8 ± 10 %) and benthos (benthic invertebrates; 2 ± 3 %). Most of the bycatch was discarded; retained bycatch only represented 4% of the total catch. Fish bycatch consisted of 54 species, dominated by representatives from the Sciaenidae, but *Stellifer microps* and *Cynoscion jamaicensis* represented 50% of the fish bycatch by weight. Most fishes in the bycatch were small, measuring around 10 cm. Bycatch of benthos included 24 benthic invertebrate taxa, dominated by brown shrimp *Penaeus subtilis*, the gastropod *Marsupina bufo* and the swimming crab *Callinectes ornatus*. Furthermore, overall catch rate and relative catch composition showed monthly variability. Both catch and bycatch rates were highest in August. Diurnal variability in overall catch rate and catch composition was small. In general, the Suriname seabob fishery produced low bycatch-to-shrimp ratios (0.81 ± 0.58) for a tropical penaeid shrimp fishery. Nevertheless, discarded bycatch included species of commercial interest for the coastal artisanal fishing fleet, notably *C. jamaicensis*, *Cynoscion virescens*, *Macrodon ancylodon* and *Nebris microps*. Several elasmobranch (Chondrichthyes: Elasmobranchii) species of conservation concern were also caught, including five species of rays and the electric ray *Narcine bancroftii*.

Worldwide, many species of elasmobranchs are currently threatened by marine fisheries activity and are on the Red List of the International Union for Conservation of Nature (IUCN). Therefore, as a species group of particular conservation concern, **Chapter 7** focused on the bycatch of rays (Elasmobranchii: Batoidea). More specifically, we addressed whether the gear adaptations currently used in the seabob fishery, Turtle Excluder Devices (TEDs) and square-mesh panel Bycatch Reduction Devices (BRDs), mitigate ray bycatch. In this study, 65 catch-comparison hauls were conducted, comparing trawls with and without gear adaptations. Trawls with a BRD and TED combination reduced ray catch rate by 36%. A 21% reduction in mean size indicated the preferential exclusion of large rays. Hence, high escape ratios were observed for *Dasyatis geijskesi* (77%), a large-sized species, while exclusion of the small species *Urotrygon microphthalmum* was not significant, although their disc width is small enough to pass through the meshes of the BRD. Furthermore, a size-dependent escape for the two most abundant mid-sized ray species *Dasyatis guttata* and *Gymnura micrura* was observed. Exclusion-at-size differed for both species, however, likely related to species-specific morphology or behavior in response to the TED. This study showed that the combination of BRD and TED caused an important reduction in ray bycatch in seabob shrimp fisheries off Suriname. The great reduction in catch

of large-sized rays is positive, but the mortality of juvenile rays is likely to have negative consequences for their populations.

Finally, **PART IV** translated scientific knowledge into management recommendations, in order to move **towards sustainable management of *X. kroyeri* fisheries in Suriname.** The management of the Suriname seabob fishery currently has measures in place related to (1) spatio-temporal operation of the fishery, (2) fishing effort, (3) gear-related aspects of the fishery and (4) governance. **Chapter 8** evaluated each of the aspects and discussed how to use the information gathered in this doctoral thesis for the further implementation of an EAF. Related to the spatio-temporal operation of the fishery, we recommended maintaining the current legal seabob trawling zone, emphasizing the importance of the trawling ban below 18 m depth in protecting the nursery function of the inshore waters. As a second spatial measure, we suggested to implement a 'move-on rule' to instantly react to excessive bycatch ratios. Currently, no temporal fishing restrictions are in place; analyzing stock dynamics should reveal whether or not temporal restrictions are required. Fishing effort is currently regulated through a Harvest Control Rule (HCR) specifying the allowable number of fishing days. Given the key wasp-waist function of *X. kroyeri* in the ecosystem, we advised to strictly adhere to the current HCR, and to update the stock assessment with available data. Further research will have to identify whether the current exploitation rate affects the role of *X. kroyeri* in the food web, or whether output control measures (e.g. catch quota) might be required. Bycatch of undersized commercial species and vulnerable elasmobranchs remains a concern for the seabob fishery. Therefore, regarding gear-related management, we recommended optimizing the fishing gear to further reduce bycatch. In this way, ecological and socio-economic consequences of bycatch mortality can be minimized. Finally, we emphasized the crucial role of the Seabob Working Group as a stakeholder's platform to seek consensus on the management measures to be taken, and to keep track of their implementation. The experience in the Suriname seabob fishery shows that MSC certification can play an important role in the practical implementation of an EAF. Nevertheless, the management of other fisheries will have to be revised as well, in order to successfully apply an EAF in Suriname.

SAMENVATTING

De ecosysteembenadering van het visserijbeheer (EBV) wordt algemeen aanzien als de beste aanpak voor het toekomstige beheer van de zeevisserij. In tegenstelling tot het traditionele 'single-species' management, erkent een EBV expliciet de complexiteit van de ecosystemen waarin visserijen actief zijn. De volgende elementen zijn daarom cruciaal in een EBV: (1) de voedselrelaties tussen beviste soorten en hun voedselbronnen, (2) indirecte interacties tussen de vissersvloten – via voedselrelaties of bijvangst - en (3) de impact van visserij op mariene habitats en soortengemeenschappen. Het negeren van deze aspecten in het visserijbeheer ligt aan de basis van verschillende milieu- en socio-economische problemen in tropische garnalen visserij. Deze visserij is wereldwijd de belangrijkste leverancier van garnalen, maar wordt geconfronteerd met een negatieve publieke perceptie. De toenemende vraag van consumenten voor duurzame visserijproducten heeft de visserij op Atlantische seabobgarnalen *Xiphopenaeus kroyeri* (Crustacea: Penaeidae) voor de kust van Suriname ertoe aangezet om stappen te ondernemen naar een duurzamere visserijmethode. Hierdoor kreeg de seabob visserij een Marine Stewardship Council (MSC) keurmerk in 2011, een belangrijke mijlpaal in de toepassing van een EBV. Niettemin, zoals werd benadrukt tijdens de MSC beoordelingen, ontbreekt er belangrijke informatie om de impact van seabob visserij op bepaalde aspecten van de structuur en het functioneren van het mariene ecosysteem grondig te evalueren. **Het doel van dit proefschrift was om relevante kennis aan te reiken die nodig is voor een betere ecosysteembenadering van het beheer van de *Xiphopenaeus kroyeri* visserij in Suriname. We hebben ons in het bijzonder gericht op (1) de karakterisering van de gemeenschappen van bodemdieren en habitats van het ondiepe continentaal plat, waar de *X. kroyeri* visserij plaatsvindt (ecosysteem structuur), (2) de rol van *X. kroyeri* in het voedselweb van de Surinaamse kustwateren (ecosysteem functioneren), (3) de impact van de *X. kroyeri* visserij op de structuur en het functioneren van het ecosysteem (ecosysteem impact) en (4) de vertaling van de wetenschappelijke resultaten in aanbevelingen voor het visserijbeheer (beheersimplicaties).**

Hoofdstuk 1 introduceert de bredere context van het proefschrift door kort in te gaan op de huidige visserijcrisis, het concept van EBV en het MSC-keurmerk. Verder worden de problemen en uitdagingen in verband met garnalenvisserij, en meer specifiek de visserij op seabobgarnalen in Suriname geschetst. Daarnaast bevat het proefschrift bevat zeven hoofdstukken, ondergebracht in vier delen, in overeenkomst met de vier doelstellingen van dit doctoraat.

Omdat ecologisch onderzoek op het Surinaamse continentaal plat in het verleden beperkt was, zijn **hoofdstukken 2 en 3** (samen **DEEL I**) gericht op het **karakteriseren van de bodemgemeenschappen in de kustwateren van**

Suriname. Daarvoor werden epibenthos, demersale vis en omgevingsparameters bemonsterd tijdens een uitgebreide campagne in 2012-2013. De gegevens werden verzameld op (twee-)maandelijkse basis op 15 locaties in het ondiepe (<40 m) kustgebied. De ruimtelijke en temporele spreiding van de epibenthische fauna werd beschreven in **Hoofdstuk 2**, samen met de abiotische karakteristieken van het ondiepe continentaal plat. Op basis van 148 sleepnet monsters werden 92 epibenthische taxa geïdentificeerd. Deze kwamen voor in drie ruimtelijk gestructureerde soortengemeenschappen, gerelateerd aan duidelijke gradiënten in een aantal milieu-parameters. Een soortenarme *kustgemeenschap*, gedomineerd door *X. kroyeri*, werd onderscheiden in een zone met modderige bodems en troebel water vlak onder de kust (6 tot 20 m diepte). In de buurt van de 30 m dieptelijn waren sedimenten veel grover (mediane korrelgrootte gemiddeld 345 ± 103 micrometer vs. 128 ± 53 micrometer in de *kustgemeenschap*) en was het water veel helderder (gemiddeld 7,6 ± 3,5 m vs. 2,4 ± 2,1 m in de *kustgemeenschap*). In deze zone werd een soortenrijke *offshoregemeenschap* gevonden, gekenmerkt door slangsterren (voornamelijk *Ophioderma brevispina* en *Ophiolepis elegans*) en een verscheidenheid aan krabben, zeesterren en heremietkreeften. Een *transitiegemeenschap* werd onderscheiden tussen de beide zones, met epibenthische soorten die doorgaans te vinden zijn in zowel de *kust-* of *offshoregemeenschap*.

De gemeenschap van demersale vis op het ondiepe Surinaamse continentaal plat **(Hoofdstuk 3)** bevatte 98 soorten. De sleepnet monsters werden echter gedomineerd door *Stellifer rastrifer, Amphiarius rugispinis* en *Cynoscion jamaicensis*, goed voor 50 % van alle gevangen vissen. In analogie met de epibenthos gemeenschap, wees de cluster analyse op het voorkomen van drie soortengemeenschappen, in een kust-offshore dieptegradient. De *kustgemeenschap* van demersale vis, aanwezig in de ondiepe troebele wateren tot 20 meter diepte, vertegenwoordigde de 'sciaeniden gemeenschap'. Deze is typisch voor ondiepe tropische kustwateren en werd gedomineerd door Sciaenidae en Ariidae. Rond 27 m waterdiepte markeerde een *transitiegemeenschap* de overgang naar een heel andere *offshoregemeenschap* van demersale vis op de diepste bemonsteringslocaties (34 m). De *offshoregemeenschap* had een significant lagere densiteit en diversiteit aan demersale vis, en bevatte vertegenwoordigers van visfamilies die typisch zijn voor diepere delen van tropische continentale plateaus, zoals Paralichthyidae, Triglidae en Lutjanidae. Hoewel duidelijke seizoensgebonden verschillen in omgevingsparameters werden geobserveerd (bijvoorbeeld droog vs. regenseizoen), werd weinig temporele variatie waargenomen in de gemeenschappen van epibenthos en demersale vis. Deze waren voornamelijk ruimtelijk gestructureerd, in een kust-offshore gradient gerelateerd aan diepte, sediment korrelgrootte en het gehalte aan organische koolstof in het sediment. De overgang van *kustgemeenschappen* naar *offshoregemeenschappen* was het belangrijkste kenmerk van de benthische fauna van het ondiepe

continentale plat van Suriname, en viel samen met een overgang tussen twee belangrijke ecosystemen: een kustgebonden systeem beïnvloed door rivieruitvloei en detritus, versus een offshore, helder-water systeem waar primaire productie door fytoplankton aan de basis ligt van het voedselweb. Demersale vissen waren abundant in het kustecosysteem, samen met een potentieel belangrijke epibenthische voedselbron, de seabobgarnaal *X. kroyeri*, die zeer hoge dichtheden bereikte (tot 1383 individuen per 1000 m^2). Verder vervullen de ondiepe kustwateren onder 20 m diepte wellicht een belangrijke kraamkamerfunctie, omdat jonge exemplaren van commercieel belangrijke demersale vissoorten veelvuldig voorkwamen in onze kustgebonden sleepnet vangsten.

Het eerste deel van het proefschrift maakte duidelijk dat *X. kroyeri* de epibenthische gemeenschappen van de kustwateren (<27 m diepte) van Suriname domineert, en dat het voorkomen van deze soort samenvalt met een soortenrijke gemeenschap van demersale vis. In **DEEL II** werd **de rol van *X. kroyeri* in het voedselweb van de Surinaamse kustwateren** bestudeerd, waarbij zowel de prooien als predatoren van de seabobgarnaal werden onderzocht. In **Hoofdstuk 4** onderzochten we de trofische ecologie van *X. kroyeri* door middel van maaganalyses en stabiele isotopen analyses. Hieruit bleek dat de seabobgarnaal een omnivoor dieet heeft, en zich opportunistisch voedt met zowel dierlijke prooien als primaire voedselbronnen. We concludeerden dat kustgebonden organische stof in de waterkolom en op de bodem, en koolstof uit rivieruitvloei en mangrove bladafval niet werden opgenomen door *X. kroyeri*, omwille van de zeer lage ^{13}C-waarden van deze potentiele voedselbronnen. Een ontogenetisch verandering in het dieet werd waargenomen tussen het postlarvaal, juveniel en adult stadium. Adulte seabobgarnalen stonden hoger in de voedselketen, en aten iets grotere bodemdiertjes zoals copepoden, amfipoden en de luciferide garnaal *Lucifer faxoni*. Deze prooien werden wellicht voornamelijk overdag gevangen wanneer ze zich bij de bodem ophouden. Bentische microalgen (BM) van intertidale slikken en offshore sedimentair organisch materiaal waren belangrijke primaire voedselbronnen voor alle levensstadia van *X. kroyeri*. Een Bayesiaans model gaf aan dat intertidale BM tot 64 % van de totale voeding van *X. kroyeri* vertegenwoordigden. Onze resultaten gaven aan dat de primaire productie op droogvallende slikken, door middel van BM, een belangrijke energiebron vormt voor het subtidale voedselweb.

De volgende stap in het bestuderen van de functionele rol van *X. kroyeri* was het beoordelen of de soort een belangrijke prooi vormt voor hogere niveaus in de voedselketen. Dit was het onderwerp van **Hoofdstuk 5**, waarin het trofische belang van *X. kroyeri* voor de demersale visgemeenschap op het ondiepe continentaal plat van Suriname werd geëvalueerd. Het dieet van 13 algemeen voorkomende vissoorten werd onderzocht door middel van maaginhoud en stabiele isotopen analyses. Atlantische seabob garnalen werden gevonden in de magen van 11 vissoorten, en de isotopische niche van de demersale

visgemeenschap overlapte aanzienlijk met de theoretische isotopische niche van een *X. kroyeri* predator. Twee trofische groepen konden worden onderscheiden: epi-piscivoren en benthivoren. De eerste groep bevatte vooral Sciaenidae, die zich voedden met zowel vis als garnalen, en met een gravimetrische bijdrage van *X. kroyeri* rond 40 %. De epi-piscivoren omvatten ook één vis specialist (*Gymnura micrura*) en twee garnalen specialisten (*Nebris microps* en *Cynoscion virescens*). De benthivoren waren taxonomisch meer divers en toonde een meer gevarieerde voeding. Hun maaginhoud bestond voor een aanzienlijk deel uit 'verteerd materiaal', deels afkomstig van *X. kroyeri*. De resultaten toonden aan dat een groot deel van de energie in het benthische voedselweb van het ondiepe Surinaamse continentaal plat wordt gekanaliseerd op het intermediaire trofische niveau in een 'wespentaille –patroon', via de abundante en productieve benthische ongewervelde *X. kroyeri*.

Terwijl de eerste twee delen van het proefschrift aspecten van de structuur en het functioneren van het ecosysteem behandelen, was **DEEL III** erop gericht **de impact van de *X. kroyeri* visserij op het kustecosysteem van Suriname te beoordelen**. De impact op de bodemgemeenschappen was de focus van **Hoofdstuk 6**, waarin de samenstelling van de vangsten van de seabob visserij in Suriname onderzocht werden. Dit werd gedaan op basis van 68 vangstmonsters, genomen zowel overdag als 's nachts op zes commerciële zeereizen tussen april en november 2014. De totale vangst bedroeg gemiddeld 205 ± 180 kg per uur slepen. De vangsten werden gedomineerd door seabob garnalen, goed voor 59 ± 13% van de totale vangst in gewicht. De bijvangst werd gedomineerd door vis (31 ± 14% van de totale vangst), gevolgd door kwallen (8 ± 10%) en benthos (benthische ongewervelden, 2 ± 3%). De meeste bijvangst werd teruggegooid; aangelande bijvangst vertegenwoordigde slechts 4% van de totale vangst. Vis bijvangst bestond uit 54 soorten, gedomineerd door vertegenwoordigers van de Sciaenidae, maar *Stellifer microps* en *Cynoscion jamaicensis* vertegenwoordigde 50% van het gewicht aan vis bijvangst. De meeste vissen in de bijvangst waren klein, in de grootteorde van 10 cm. In de benthos bijvangst werden 24 benthische ongewervelde taxa onderscheiden, gedomineerd door de garnaal *Penaeus subtilis*, de gastropode *Marsupina bufo* en de zwemkrab *Callinectes ornatus*. Verder vertoonden de totale vangsten en de samenstelling van de vangsten temporele variabiliteit. Zowel de vangsten als bijvangst-ratios waren het hoogst in augustus. Dag-nacht verschillen in de totale vangsten en samenstelling van de vangst waren klein. In het algemeen produceerde de Surinaamse seabob visserij lage bijvangst-vangst ratios (0,81 ± 0,58) in vergelijking met andere tropische penaeide garnalenvisserijen. De teruggegooide bijvangst bevatte niettemin soorten van commercieel belang voor de artisanale kustvisserij in Suriname, met name *C. jamaicensis, Cynoscion virescens, Macrodon ancylodon* en *Nebris microps*. Verder werden verschillende kwetsbare soorten kraakbeenvissen (Chondrichthyes: Elasmobranchii) gevangen, waaronder vijf soorten roggen en de elektrische rog *Narcine bancroftii*.

Wereldwijd zijn vele soorten kraakbeenvissen momenteel bedreigd door visserij activiteiten, en staan op de Rode Lijst van de International Unie voor Natuurbescherming (IUCN). Daarom richtte **Hoofdstuk 7** zich op de bijvangst van roggen (Elasmobranchii: batoidea). Meer in het bijzonder behandelden we de vraag of de netaanpassingen die momenteel gebruikt worden in de seabob visserij, 'Turtle Excluder Devices' (TEDs) en 'Bycatch Reduction Devices' (BRDs), effectief zijn in het verminderen van de bijvangst van roggen. In deze studie werden 65 vangstvergelijkingen uitgevoerd, waarbij netten met en zonder aanpassingen werden vergeleken. Sleepnetten met een BRD en TED combinatie verlaagden de roggen bijvangst met 36%. Een reductie van 21% in de gemiddelde grootte van roggen gaf aan dat vooral grote roggen konden ontsnappen uit de netten. Een groot aandeel (77%) van de grote soort *Dasyatis geijskesi* kon ontsnappen, terwijl uitsluiting van de kleinere soort *Urotrygon microphthalmum* niet significant was, hoewel deze in theorie klein genoeg was om door de mazen van de BRD te glippen. Verder werd een grootte-afhankelijke ontsnapping waargenomen voor de twee meest abundante middelgrote roggensoorten *Dasyatis guttata* en *Gymnura micrura*. Beide soorten vertoonden echter een verschillende grootte-afhankelijke ontsnapping, waarschijnlijk gerelateerd aan soortspecifieke morfologie of gedrag in reactie tot de TED. Deze studie toonde aan dat de combinatie van de BRD en TED een belangrijke vermindering van roggen bijvangst veroorzaakt in de seabob garnalenvisserij in Suriname. De aanzienlijke vermindering van de vangst van grote roggen is positief, maar sterfte van juveniele roggen kan negatieve gevolgen hebben voor hun populaties.

Tot slot vertaalde **DEEL IV** de wetenschappelijke kennis verzameld in dit doctoraat naar concrete aanbevelingen, met als doel **een duurzaam beheer van de *X. kroyeri* visserij in Suriname te ondersteunen**. Het beheer van de Surinaamse seabob visserij heeft momenteel maatregelen genomen met betrekking tot (1) de ruimtelijk-temporele werking van de visserij, (2) de visserij-inspanning, (3) technische aspecten van de visserij en (4) het bestuur. **Hoofdstuk 8** evalueerde elk van deze aspecten, en besprak hoe de informatie verzameld in dit proefschrift kan gebruikt worden voor de verdere implementatie van een EAF. Met betrekking tot de ruimtelijk-temporele werking van de visserij stelden we voor om de huidige wettelijke seabob visserij zone te handhaven. Hierbij benadrukten we het belang van het verbod op sleepnetvisserijen in minder dan 18 meter waterdiepte in het beschermen van de kraamkamerfunctie van de kustwateren. Als tweede ruimtelijke maatregel stelden we voor om een 'move-on rule' te implementeren om direct te kunnen reageren op overmatige bijvangst ratios. Momenteel zijn er geen temporele vangstbeperkingen voor de visserij; het analyseren van temporele populatiepatronen moet uitwijzen of temporele visserij regulatie vereist is. De visserij-inspanning in de seabob visserij wordt momenteel geregeld door middel van een 'Harvest Control Rule' (HCR), die het toegestane aantal visdagen specifieert. Gezien de cruciale trofische functie van *X. kroyeri* in het

ecosysteem, adviseerden we om strikt te houden aan de huidige HCR, en de HCR te herevaluaren op basis van alle beschikbare gegevens. Verder onderzoek zal moeten uitwijzen of het huidige niveau van exploitatie de rol van *X. kroyeri* in het voedselweb beïnvloedt, of dat bijkomende output-beheersmaatregelen (bv. vangstquota) nodig zijn. Bijvangst van ondermaatse commerciële soorten en kwetsbare kraakbeenvissen blijft een belangrijk aandachtspunt voor de seabob visserij. Daarom, met betrekking tot visserijtechnisch management, raadden we aan om het vistuig te optimaliseren om zo de bijvangst verder terug te dringen. Op deze manier kunnen ecologische en socio-economische gevolgen van bijvangst en teruggooi worden geminimaliseerd. Tot slot benadrukten we de cruciale rol van de Seabob Werkgroep als platform om alle belanghebbenden in de visserij samen te brengen, consensus te bereiken over de te nemen maatregelen, en de uitvoering ervan op te volgen. De ervaring in de Surinaamse seabob visserij toont aan dat MSC certificering een belangrijke rol kan spelen bij de praktische implementatie van een EAF. Toch zal het beheer van andere visserijen ook herzien moeten worden , om tot een succesvolle toepassing van een EAF te komen in Suriname.

POPULAIRE SAMENVATTING

Ecosysteembenadering van het Visserijbeheer (EBV) wordt algemeen aanzien als de beste manier om onze levende mariene hulpbronnen te beheren. Terwijl traditioneel visserijbeheer zich enkel richt op de populaties van de beviste soorten, erkent een EBV de complexiteit van ecosystemen waarin visserijen actief zijn. Cruciale aspecten van een EBV zijn daarom (1) voedselrelaties tussen beviste soorten, hun prooien en predatoren, (2) indirecte interacties tussen verschillende vissersvloten – via voedselrelaties en bijvangst – en (3) de impact van visserij op mariene leefgebieden en soortengemeenschappen. Het negeren van deze elementen in het visserijbeheer ligt aan de basis van verschillende milieu- en socio-economische problemen, met name in de tropische garnalenvisserij.

Ondanks de groei van aquacultuur, wordt 60% van de garnalen nog steeds in het wild gevangen, voornamelijk in tropische kustzeeën. De tropische garnalenvisserij is daarmee wereldwijd de belangrijkste leverancier van garnalen. Deze visserij staat echter in een slecht daglicht, vooral vanwege het grote aandeel ongewenste bijvangst dat samen met de garnalen wordt opgevist. Deze bijvangst bestaat vaak uit jonge exemplaren van commerciële vissoorten, waardoor garnalenvisserij ongewenst een negatief effect heeft op andere, vaak kleinschalige, visserijen in de regio. Zeeschildpadden, roggen en haaien kunnen echter ook in de bijvangst voorkomen, wat de populaties van deze kwetsbare soorten in gevaar brengt. De tropische garnalenvisserij zou dus veel baat hebben bij een ecosysteembenadering van het beheer.

De zorgwekkende toestand waarin veel visbestanden zich bevinden, en de nood aan een beter visserijbeheer dringt ook steeds meer door bij de consument, die van zich laat horen via een toenemende vraag naar duurzame visserijproducten. In Suriname was dit de aanleiding tot initiatieven ter verduurzaming van de visserij op Atlantische seabobgarnalen *Xiphopenaeus kroyeri,* die vooral in Europa geconsumeerd worden. De seabobvisserij verkreeg hierdoor in 2011 een ecologisch keurmerk van de Marine Stewardship Council (MSC), het meest gekende eco-label in de visserij. Het keurmerk was in dit geval geen eindpunt, maar de start van een traject voor verdere verbetering. Tijdens de MSC beoordelingen werd namelijk benadrukt dat er belangrijke informatie ontbrak om de impact van seabobvisserij op de structuur en de werking van het mariene ecosysteem grondig te evalueren. Deze kennishiaten vormden de directe aanleiding tot dit onderzoeksproject, met als doel het **aanreiken van relevante kennis voor een verbeterde ecosysteembenadering van het beheer van de seabobvisserij in Suriname.** Dit alles in nauwe samenwerking met het lokale visserijbeheer, de industrie, ngo's en de lokale universiteit.

HET ONDERZOEK: OVER VISSEN, VOEDSELWEBBEN EN VANGSTEN

Het kustecosysteem in Suriname was tot voor kort een quasi blinde vlek voor mariene biologen. Het onderzoek richtte zich in de eerste plaats dan ook op het in kaart brengen van ruimtelijke patronen van ongewervelden en vissen in de kustwateren van Suriname. Er was een duidelijke overgang merkbaar tussen twee verschillende ecosystemen parallel aan de kustlijn. Het water vlak onder de kust is sterk beïnvloed door rivieruitvloei, waardoor de bodem er modderig en het water erg troebel is. Hoewel in dit 'estuariene' kustsysteem meer dan 60 soorten bodemvissen voorkomen, is de gemeenschap van ongewervelde bodemdieren er erg soortenarm, met de seabobgarnaal als enige dominante soort. Rond de dieptelijn van 30 m is een drastische verandering merkbaar naar een meer 'oceanisch' systeem, gekenmerkt door zanderige bodems en helderder water. Hier werden minder soorten vis aangetroffen, maar de bodem wordt bevolkt door een soortenrijke gemeenschap van ongewervelden, waaronder slangsterren, krabben, zeesterren en heremietkreeften. Seabobgarnalen worden dus vooral gevonden dicht bij de kust, en wel in bijzonder hoge aantallen: tot 1383 garnalen per 1000m². Die kustzone doet ook dienst als kraamkamer voor de talrijk aanwezige bodemvissen.

Uit dieetanalyses blijkt dat seabobgarnalen omnivoor zijn, en dus zowel plantaardig als dierlijk materiaal verorberen. Toch zijn ze vrij kieskeurig want voedselbronnen met een lage voedingswaarde, zoals bijvoorbeeld bladafval van mangroves, laten ze links liggen. Het meeste voedsel (tot 64%) halen ze uit microscopische algen die op slikken in de intergetijdenzone groeien. Daarnaast eten ze ook roeipootkreeftjes, vlokreeftjes en lucifergarnaaltjes (*Lucifer faxoni*). Seabobgarnalen staan op hun beurt op het menu bij tenminste 11 van de 13 meest voorkomende vissoorten. We konden een onderscheid maken tussen vis- en garnaleneters en bodemvoedende vissen. Bij de eerste groep maken seabobgarnalen ongeveer 40% uit van het dieet en sommige van deze vissen zijn echt gespecialiseerde garnaleneters. De tweede groep, de bodemvoedende vissen hebben een meer gevarieerd dieet, maar seabobgarnalen vormen opnieuw een aanzienlijk deel van de opgenomen voeding. Deze resultaten tonen aan dat de seabobgarnaal een sleutelfunctie heeft binnen het voedselweb, omdat ze de energie kanaliseert van de basis van het voedselweb naar het hoger niveau van de predatoren.

Via analyse van de vangsten uit de commerciële seabobvisserij, werd een inschatting gemaakt van de impact van dit type visserij op het ecosysteem. Per uur slepen werd gemiddeld 205 kg vangst genoteerd, waarvan gemiddeld 59% bestond uit seabobgarnalen. De resterende 41%, de bijvangst, bestond vooral uit vis, kwallen en ongewervelde bodemdieren. De meeste vissen in de bijvangst waren klein, in de orde van 10 cm. Het overgrote deel van de bijvangst werd teruggegooid, waardoor gemiddeld 63% van de totale vangst werd aangeland. Dat lijkt weinig, maar binnen de tropische garnalenvisserij scoort de Surinaamse seabobvisserij erg goed met per kg gevangen seabobgarnalen gemiddeld 0.8

kg bijvangst. De teruggegooide bijvangst bevatte niettemin vissoorten van commercieel belang voor de artisanale kustvisserij in Suriname en er werden verschillende kwetsbare soorten kraakbeenvissen gevangen, waaronder vijf soorten roggen en de elektrische rog *Narcine bancroftii*. Om bijvangsten van kwetsbare soorten te verminderen worden in de seabobvisserij nu al 'Turtle Excluder Devices' (TEDs) en 'Bycatch Reduction Devices' (BRDs) ingebouwd in de visnetten. Via vangstvergelijkingen gingen we na of die ook effectief werken. Uit de resultaten blijkt dat sleepnetten met een BRD- en TED-combinatie de bijvangst van roggen verlaagden met 36%. Vooral grote roggen konden ontsnappen uit de netten. De aanzienlijke vermindering van de vangst van grote roggen is positief, maar sterfte van juveniele roggen kan negatieve gevolgen hebben voor hun populaties.

VAN WETENSCHAP TOT VISSERIJBEHEER

De Surinaamse seabobvisserij heeft in functie van het MSC-label al verschillende maatregelen genomen waaronder een afgebakende visserijzone, een maximum toegelaten visserij-inspanning, aangepaste visnetten met TED en BRD en een overlegplatform voor alle belanghebbenden. Op basis van de resultaten van dit onderzoek stellen we voor dat de afgebakende visserijzone gehandhaafd blijft. Vooral het huidige verbod op sleepnetvisserijen in minder dan 18 meter waterdiepte moet bestendigd worden voor het behoud van de kraamkamer- en opgroeifunctie van de kustwateren. Verder zou een 'move-on rule' geïmplementeerd kunnen worden, waarbij wordt gestopt met vissen in een bepaald gebied als het aandeel van de bijvangst te groot wordt. De visserij-inspanning in de seabobvisserij wordt momenteel geregeld door middel van een 'Harvest Control Rule' (HCR), die het toegestane aantal visdagen specifieert op basis van de vangsten. Gezien de cruciale rol van de seabobgarnaal in het voedselweb adviseren we om strikt te houden aan de vangstbeperkingen opgelegd door de huidige HCR en de HCR te her-evalueren op basis van alle beschikbare gegevens. Verder onderzoek zal moeten uitwijzen of de huidige visserijdruk de rol van de seabobgarnaal in het voedselweb beïnvloedt en of eventueel bijkomende beheersmaatregelen (bv. vangstquota) nodig zijn. Ook bijvangst van ondermaatse commerciële soorten en kwetsbare kraakbeenvissen blijft een belangrijk aandachtspunt voor de seabobvisserij. Daarom moet werk gemaakt worden van vistuig dat bijvangst nóg verder kan terugdringen. Tot slot benadrukken we de cruciale rol van de Seabob Werkgroep in het beheer van de visserij. Dit platform brengt alle belanghebbenden in de visserij samen, buigt zich over de te nemen maatregelen en volgt de uitvoering ervan op.

Het toepassen van een ecosysteembenadering in het visserijbeheer wordt vaak gezien als een complexe en bijna onmogelijke opgave. Het traject van de seabobvisserij toont aan dat we dit proces niet moeten zien als een revolutie maar een evolutie, waarbij verandering gebeurt in kleine stappen en er gestreefd wordt naar continue verbetering. Participatief beheer, waarin alle

belanghebbenden hun zeg hebben, is hierbij cruciaal, evenals betrouwbare informatie en onderzoek. De Surinaamse seabobvisserij laat zien dat eco-labeling een katalyserende rol kan spelen in de toepassing van een ecosysteembenadering. Het MSC label was een belangrijke mijlpaal in de verduurzaming van deze visserij, maar er is nog ruimte voor verbetering. De resultaten van dit onderzoek kunnen daartoe de wetenschappelijke basis vormen.

LIST OF ABBREVIATIONS

AFDW	Ash-free Dry Weight
AIC	Akaike Information Criterion
BIC	Bayesian Information Criterion
BM	Benthic Microalgae
BRD	Bycatch Reduction Device
CHL	Chlorophyll (a)
CPUE	Catch-per-unit-effort
CRFM	Caribbean Regional Fisheries Mechanism
DAS	Days-at-sea
DistLM	Distance-based Linear Models
DW	Dry Weight
EAF	Ecosystem Approach to Fisheries
EBFM	Ecosystem Based Fisheries Management
EBM	Ecosystem Based Management
EEZ	Exclusive Economic Zone
EwE	Ecopath with Ecosim
FAO	Food and Agriculture Organization of the United Nations
FSC	Forest Stewardship Council
GC	Guiana Current
GLMM	Generalized Linear Mixed Model
HCR	Harvest Control Rule
ITCZ	Inter-tropical Convergence Zone
IUCN	International Union for Conservation of Nature
LVV	Ministry of Agriculture, Animal husbandry and Fisheries
MC	Monte Carlo
MEDSAND	Median grainsize of sediment sand fraction
MSC	Marine Stewardship Council
MUD	Sediment mud content
NBC	North Brazil Current
NECC	North Equatorial Counter Current
NGO	Non-governmental Organisation
nMDS	non-metrical Multidimensional Scaling
PCO	Principal Coordinate Analysis
PERMANOVA	Permutational Analysis of Variance
PI	Performance Indicator
POM	Particulate Organic Matter
RV	Research Vessel
SD	Standard Deviation
SE	Standard Erros
SEA	Standard Ellipse Area
SECCHI	Secchi depth
SF-TSM	Surface Total Sustpended Matter
SI	Stable Isotope
SIAR	Stable Isotope Analysis in R
SIBER	Stable Isotope Bayesian Ellipses in R
SIMPER	Similarity Percentages
SIMPROF	Similarity Profile
SOM	Sedimentary Organic Matter
sPOM	Suspended Particulate Organic Matter
SST	Sea Surface Temperature
SS-TSM	Sub-surface Total Suspended Matter
STD	Salinity - Temperature - Depth
SWG	Seabob Working Group
TED	Turtle Excluder Device
TOC	Total Organic Carbon
TSM	Total Suspended Matter
UN	United Nations
VMS	Vessel Monitoring System
WW	Wet Weight
WWF	World Wide Fund for Nature

1

GENERAL INTRODUCTION

The Ecosystem Approach to Fisheries (EAF) is widely acknowledged as being the best approach to future fisheries management (FAO, 2016a). The massive expansion of marine fisheries in the 20th century has caused both environmental and socio-economic problems and challenges (Pauly, 2006). Fisheries have been managed under a expansionist economic model, evidenced by an open-access policy and disregard of the catch limits set by fisheries biologists (Roberts, 1997; Rees, 2002). The current global fisheries crisis makes clear that fisheries resources are limited, and should be managed by adopting an ecological economics worldview. Development of an EAF explicitly recognizes the complexity of ecosystems in which fisheries operate; however, the practical implementation of this concept remains complex and requires detailed information on the structure and functioning of the marine ecosystem that support the fisheries (Pikitch et al., 2004; Sagarin and Crowder, 2009).

Tropical shrimp trawl fisheries are the main supplier of shrimp to the global market, but these fisheries face several environmental and socio-economic problems (Gillett, 2008).The negative perception of tropical shrimp and the increasing market demand for sustainable seafood products has triggered the Atlantic seabob shrimp Xiphopenaeus kroyeri *fisheries off the coast of Suriname to take steps towards more environmentally sustainable fishing practices. This led to the seabob fishery obtaining a Marine Stewardship Council (MSC) ecolabel in 2011, which is already a major step towards the implementation of an EAF. However, sound scientific information on the coastal ecosystem and the ecological impact of the fishery is still missing, a gap largely filled by this doctoral study.*

In this introductory chapter, a brief overview is given on the current fisheries crisis, the EAF concept and the MSC ecolabel. Secondly, the problems and challenges related to shrimp fisheries and more specifically for Atlantic seabob shrimp Xiphopenaeus kroyeri *in Suriname are outlined. Finally, the aim and main objectives of this study and the outline of the thesis are presented.*

1 AN ECOSYSTEM APPROACH TO MARINE FISHERIES MANAGEMENT

1.1 FISHING MORE, CATCHING LESS: WORLD FISHERIES IN CRISIS

Marine fisheries have substantial social and economic importance. Fisheries provide food, employment and livelihood for hundreds of millions of people worldwide, mainly in coastal areas of developing world countries (Garcia and De Leiva Moreno, 2003). Despite the growing contribution of farmed seafood, wild-caught fish and invertebrates (henceforth 'fish') currently represent 57% of the direct global fish supply (FAO, 2014b), but even aquaculture still mainly relies indirectly on fisheries as well, as a source of fishmeal and –oil (Merino et al., 2012).

The public perception of marine fisheries is that they are in crisis, and have been for some time (Beddington et al., 2007). Indeed, despite an increasing demand for fish, global landings from marine capture fisheries have been decreasing for 20 years, and an increasing proportion of the catches originates from fully exploited or overfished stocks, which currently accounted for ca. 90% of the landings (FAO, 2014b).

Depletion of marine fish stocks is a relatively recent phenomenon. Despite the localized overexploitation of fish populations in inland and coastal waters (Ludwig et al., 1993), most marine fish stocks have largely been left unexploited throughout human history, protected by the size and hostility of the ocean (Roberts, 2010). In the aftermath of the Industrial Revolution, fisheries, and therefore our impact on marine fish stocks, have changed drastically (Jackson et al., 2001). In the early 19th century, steam trawlers gradually started replacing sailing vessels. These trawlers were soon rendered more effective by power winches and after World War I, diesel engines. After World War II, industrialization of fishing intensified with the introduction of freezer trawlers, radar, and acoustic fish finders (Pauly, 2006). These developments allowed marine fisheries to expand to ever deeper and more distant waters, operating on a historically unprecedented scale (e.g. Swartz et al., 2010).

Through the enormous capacity increase and innovations in fishing technology, the coastal waters of industrialized countries became rapidly overfished and commercial fisheries shifted to more distant, deeper waters (Morato et al., 2006; Swartz et al., 2010). As this was insufficient to meet the increasing demand for fish in the northern hemisphere, commercial fisheries gradually moved to the South, where many developing countries – who needed cash to repay their debts - sold their fishing access rights to developed countries (Pauly et al., 2005). This has led to many coastal areas

in the southern hemisphere being overfished by the industrialized world, resulting in depleted fish stocks for small-scale and artisanal fisheries (Mathew, 2003) as seen in numerous African countries (e.g. Atta-Mills et al., 2004).

The expanding marine fishing fleet has also increasingly impacted the status of marine ecosystems. Bottom trawling might have a severe impact on benthic habitats and communities, especially in the deep sea (e.g. Watling and Norse, 1998; Thrush and Dayton, 2002; Kaiser et al., 2002; Mangano et al., 2013). Due to overfishing of large piscivorous fishes, fisheries have gradually moved towards smaller invertebrates and planktivorous fishes. This trend, known as 'fishing down the food web', is evidenced by a steady decline in mean trophic level of global fisheries landings in recent decades, and implies a major fisheries-induced change in the structure of marine food webs (Pauly et al., 1998; Essington et al., 2006). Further, the accidental capture and mortality of non-target species (bycatch) is of major concern as it causes both environmental and socio-economic problems (e.g. Hall et al., 2000; Stevens et al., 2000; Benoit et al., 2013; Gillett, 2008).

Local stock collapses, degradation of the marine ecosystem and socio-economic problems have been caused by the massive scale increase in marine fisheries. Despite these negative effects, increased fishing effort led in general to increased catches throughout the 20th century, creating the widespread misperception of the sea as an inexhaustible source of fish (Pauly, 2006). However, the last two decades have seen a global decline in catches. According to the FAO (FAO, 2014b), the total catch of marine fisheries has declined from 86.4 million tons in 1996 to 74.4 million tons in 2010, a decline of 12 million tons. While the decline is relatively small (0.7% year^{-1}), this catch is obtained from ever-expanding fisheries and ever-increasing fishing effort (Fig. 1). In turn, a marked decline in the catch-per-effort of global fisheries has been observed since the mid-1990s, clearly signaling the unsustainable nature of today's fisheries.

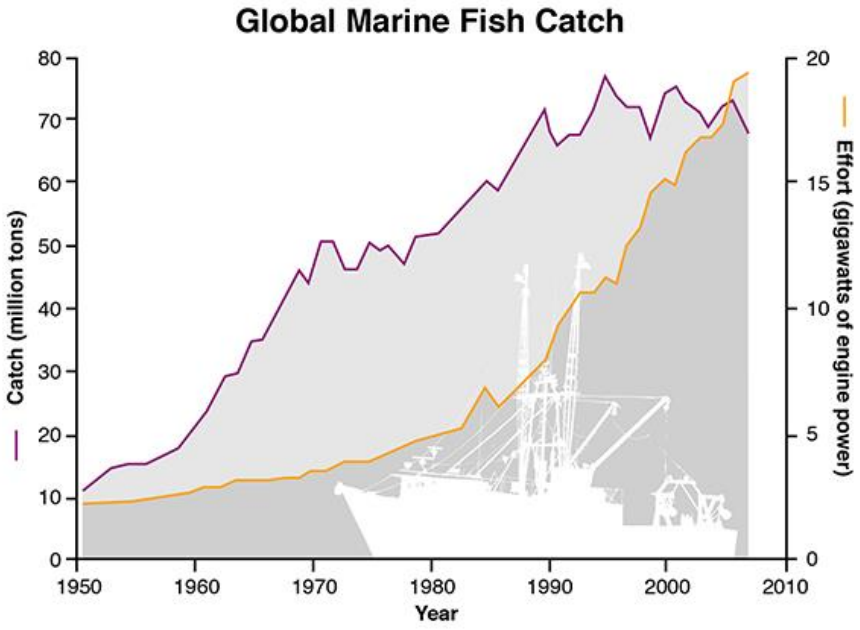


Figure 1. Beyond 'peak fish': global catches from marine fisheries (left hand axis; purple line) have massively increased since the 1950s, but they show a declining trend since the mid-1990s. Decreasing catches despite ever-increasing fishing effort (right hand axis; orange line) is a major indicator for the current crisis in marine capture fisheries (source: www.seaaroundus.org).

1.2 PLACING FISHERIES IN THEIR ECOSYSTEM CONTEXT

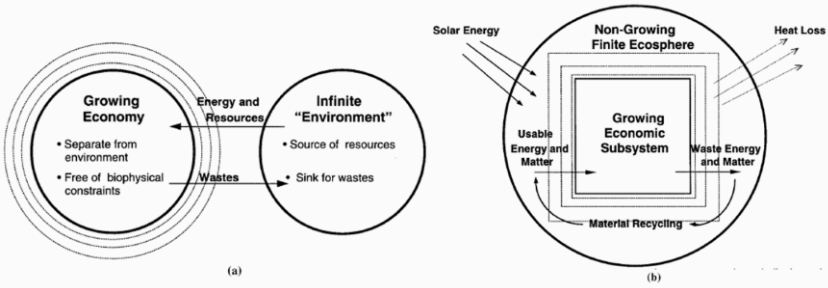
Many traditional economists claim that resource depletion is of little or no consequence because trade and technology will continue to 'push back' the limits to economic growth indefinitely (Jones, 2007). This economic paradigm, referred to as 'expansionist thinking', has been driving world development since the Industrial Revolution (Rees, 2002), and is manifested in fisheries management in two important aspects. First, while optimal levels of fishing effort to ensure 'maximum sustainable yield' have traditionally been available for many fish stocks, these catch restrictions have rarely been applied correctly (Roberts, 1997; Pauly et al., 2002). Effective fishing effort has mostly exceeded the advised levels, with direct economic gains winning over long-term benefits (e.g. Karagiannakos, 1996). Second, an 'open-access' policy applies to many fish stocks in international waters, meaning that the resources are available for anyone to exploit and profit from. This has caused a 'race for fish', and a true 'tragedy of the commons' on the world's high seas (e.g. Costello et al., 2008; McWhinnie, 2009).

The history of global fisheries has made clear that this approach to fisheries management has largely failed to provide long-term sustainable benefits. Nevertheless, fish stocks are living resources with the inherent potential to produce sustainable yields in the long run. The failure of fisheries management has left many fish stocks depleted - for some, the harm seems to be irreversible. For example, cod stocks off Newfoundland, Canada collapsed in the early 1990s, but still show no sign of recovery despite a fishing moratorium (Hutchings and Myers, 1994; Bundy and Fanning, 2005). On the other hand, many fish stocks have bounced back relatively quickly after being temporarily exempted from fishing (e.g. Dickey-Collas et al., 2010). A reduction in fishing effort can allow fish stocks to rebuild, causing higher catches on the long term. Indeed, while the world's oceans have reached their maximum production under the current fishing regime (Garcia and De Leiva Moreno, 2003), fish catches worldwide are not as high as they could potentially be under optimal fisheries management (Pauly, 2002). Proper management of fish stocks has enormous potential to increase fisheries yields from the oceans. Although fisheries management has historically been ineffective, it is not too late to turn the tide and choose a path of sustainability (Martinet et al., 2007). Fisheries scientists now widely agree that this can only be achieved by abandoning 'expansionist thinking' and instead applying 'ecological economics' to fisheries (Rees, 2002; Garcia et al., 2003; Farber et al., 2006) (see Box 1). In other words, we need an 'ecosystem approach' to fisheries.

The Ecosystem Approach to Fisheries (EAF) is also referred to as Ecosystem-Based Fisheries Management (EBFM) or simply Ecosystem-Based Management (EBM). Despite the differences in terminology (Box 2), all ecosystem-based approaches to the management of economic activities explicitly recognize the complexity of ecosystems and the interconnections among their component parts (Kimball, 2001). In practice, an EAF requires that policy makers take a wide range of fisheries impacts into account when setting objectives, supported by scientific knowledge (Jennings, 2005). Unlike traditional single-species management, the EAF goes beyond the effects of fisheries on the target species and considers the ecosystem-wide effects of fishing (e.g. Pikitch et al., 2004).

BOX 1. ECOLOGICAL ECONOMICS

Ecological economics is a science that investigates the interaction between human beings and the natural world, in other words, it studies how economic and environmental issues interact. The basic idea is that the earth is a thermodynamically closed system: it receives energy from the sun and discharges heat into space, but it cannot exchange matter with it. As a result, the quantity of matter (raw material) available to the economy is limited (Jones, 2007). In the ecological economics worldview, the economy is not considered as separate from the 'environment', but rather as an integrated, completely enclosed, and fully dependent growing sub-system of a non-growing ecosphere. In thermodynamic terms, nature is the producer and the economy the consumer: the economy requires a continuous flow of energy and material inputs from nature to sustain the production of goods and services (Daly, 1992; Rees, 1995).



Contrasting economic paradigms. (a) Classical expansionist economics treat the economy as an open, growing, independent system lacking 'connectedness' to the environment. (b) Ecological economics sees the economy as an open, growing but fully dependent subsystem of a materially-closed, non-growing, finite ecosphere (source: Rees, 2003).

Marine fishes and invertebrates are embedded in complex ecosystems. Both structure and functioning of those ecosystems can be affected by fisheries (Jennings and Kaiser, 1998; Blaber et al., 2000). Structural impacts include the physical damage done to the seabed by bottom trawling (e.g. Watling and Norse, 1998), which alters or destroys the habitat supporting the exploited resources (Kaiser et al., 2002). Further, poorly selective fishing activities generate bycatch of non-target organisms, which are often discarded. Bycatch of threatened species is a major conservation concern, while discarded commercial fishes might create socio-economic conflicts among fishing fleets and raise ethical concerns on the wastage of food (e.g. Hall et al., 2000). Fisheries also affect ecosystem functioning by modifying trophic networks and the flow of biomass (and energy) across the ecosystem

(Pauly et al., 1998; Branch et al., 2010). This can lead to trophic cascades (Frank et al., 2005; Casini et al., 2009), and ultimately to regime shifts (Daskalov et al., 2007). Considering these various indirect impacts of fishing, according to Pauly and Chuenpagdee (2002) an EAF should at least take into account:

1) The trophic relationships between exploited species and the food sources on which they rely;

2) The competition between fishing fleets, which might be expressed through bycatch or trophic linkages between species targeted by different fleets operating in the same ecosystem;

3) The direct and indirect impacts of fishing on habitats and species communities.

The concept of EAF has gained wide acceptance among scientists, and is being increasingly referred to in policy (e.g. Garcia and Cochrane, 2005). Still, the practical implementation of an EAF seems a complex task, leaving managers uncertain as to how to implement an EAF in the real world (Sagarin and Crowder, 2009). According to the FAO (Garcia et al., 2003), the EAF is the appropriate and practical way to fully implement the FAO Code of Conduct for Responsible Fisheries. This code consists of a collection of principles, goals and elements for action to achieve environmental and social sustainability in fisheries (FAO, 1995). Nevertheless, like all management frameworks, EAF is a people-based process, and stands or falls with the actions taken by stakeholders (FAO, 2016a).

Fisheries are typically managed by policymakers who are trying to seek a consensus between scientific recommendations and (short-term) economic interests of the fishing industry (Pontecorvo, 2003). In recent years, however, the fishing sector itself is increasingly taking initiatives towards environmentally sustainable exploitation. This is mainly triggered by an increased consumer awareness of the poor state of global fisheries, and a resulting market demand for products originating from sustainably managed fisheries (Jacquet et al., 2010a). Eco-labeling schemes, among which the Marine Stewardship Council (MSC; Box 3) is the best-known and respected, give market credibility to sustainable fishing practices (Gulbrandsen, 2009; Froese and Proelss, 2012). The MSC has been criticized on several aspects, including its sustainability standard, methodology, and the difficulty of small-scale fisheries to participate in the program, related to the high cost of MSC-certification (e.g. Christian et al., 2013). Although an ecological improvement process indeed involves extra costs for the fishery, eco-labeling generally enhances the economic value of the product at the end of the food chain (Jacquet and Pauly, 2007). Essentially, ecolabels set principles and criteria for sustainable fisheries that a fishery must comply with in order to obtain the

label. In this way, eco-labeling can play an important role in the practical implementation of an EAF.

BOX 2. DEFINING THE ECOSYSTEM APPROACH TO FISHERIES

The term '**ecosystem approach**' was used for the first time during the 1992 UN Convention on Biological Diversity (CBD), and was defined as '*a strategy for the integrated* management *of land, water and living resources that promotes conservation and sustainable use in an equitable way'* (CBD, 2000).

The application of the ecosystem approach in fisheries is often referred to as **'Ecosystem-Based Fisheries Management'** (EBFM), defined as '*an approach that takes major ecosystem components and services - both structural and functional - into account in managing fisheries. It values habitat, embraces a multispecies perspective, and is committed to understanding ecosystem processes. Its goal is to rebuild and sustain populations, species, biological communities and marine ecosystems at high levels of productivity and biological diversity so as not to jeopardize a wide range of goods and services from marine ecosystems while providing food, revenues and recreation for humans.*' (US National Research Council, 1998).

EBFM might be interpreted as that the ecosystem becomes the new foundation of fisheries management, and that environmental considerations should be given pre-eminence over socio-economic and cultural ones, raising concern about equity, political as well as socio-economic costs and feasibility (Garcia et al., 2003). Therefore, the FAO adopted the term '**Ecosystem Approach to Fisheries**' (EAF) , defined as '*an extension of conventional fisheries management recognizing more explicitly the interdependence between human well-being and ecosystem health and the need to maintain ecosystems productivity for present and future generations, e.g. conserving critical habitats, reducing pollution and degradation, minimizing waste, protecting endangered species*' (Ward et al., 2002). In the notion that sustainability in fisheries is indeed not limited to environmental concerns, but includes social and economic aspects as well (e.g. Kinds et al., 2016), the term 'Ecosystem Approach to Fisheries (EAF)' was adopted in this PhD thesis.

BOX 3. THE MARINE STEWARDSHIP COUNCIL (MSC)

The Marine Stewardship Council (MSC) was founded in 1997. In response to the global fisheries crisis, the World Wide Fund for Nature (WWF) teamed up with the global corporation Unilever, at that time the world's largest purchaser of frozen fish, to establish a certification scheme in the fisheries sector, akin to the Forest Stewardship Council (FSC). Inspired by the success of the FSC, the idea was to use market forces to encourage behavioral changes in fisheries. In 1999, the MSC became an independent non-profit organization, based in London (Sutton, 1996; Gulbrandsen, 2009).

The MSC developed a set of principles and criteria through an inclusive consultation process between 1996 and 1999. This consultation, involving more than 300 organizations and individuals, included two expert drafting sessions, and a series of international workshops in various regions around the world. The criteria were built on the Code of Conduct for Responsible Fisheries of the UN Food and Agriculture Organization (FAO), on the UN Fish Stocks Agreement, and on other international fisheries agreements, and they are focused around three main principles (Gulbrandsen, 2009).

Principle 1: Sustainable fish stocks. The fishing activity must be at a level which is sustainable for the fish population. Any certified fishery must operate so that fishing can continue indefinitely and is not overexploiting the resources.
Principle 2: Minimizing environmental impact. Fishing operations should be managed to maintain the structure, productivity, function and diversity of the ecosystem on which the fishery depends.
Principle 3: Effective management. The fishery must meet all local, national and international laws and must have a management system in place to respond to changing circumstances and maintain sustainability.

In order to be certified, fishery clients will appoint an accredited certification body to assess their practices against the MSC standard. The process involves a pre-assessment evaluation of the fishery, full assessment and further annual surveillance to assess compliance with MSC standard. Additionally, the chain from 'boat to plate' must be certified for traceability (Chain of Custody Certification) (MSC, 2016). As of March 2016, 283 fisheries in over 30 countries were MSC certified, accounting for 8.8 million tons of seafood annually or nearly 10% the total global wild-caught seafood supply. There are currently more than 20,000 products with the MSC ecolabel available to consumers in 100 (MSC, 2016).

2 CASE STUDY: TRAWL FISHERIES FOR ATLANTIC SEABOB SHRIMP *XIPHOPENAEUS KROYERI* IN SURINAME

2.1 SHRIMP TRAWL FISHERIES

Worldwide, shrimp is one of the most important fishery products in terms of economic value, worth over 10 billion USD, which accounts for 16% of the total value of internationally traded fishery exports (Gillett, 2008). The world production of shrimp is currently around 6 million tons. Despite a growing aquaculture sector, about 60% of shrimp production in the world originates from capture fisheries (Gillett, 2008). About 70% of the world's wild caught shrimp production is realized in tropical and subtropical nearshore areas, where shrimp fisheries mainly target penaeids (Crustacea: Penaeidea), which occur abundantly on soft-bottom habitats (Alongi, 1989; FAO, 1999). Despite their economic importance, tropical penaeid shrimp fisheries face many problems associated with the ecological and socio-economic effects of fishing (EJF, 2003).

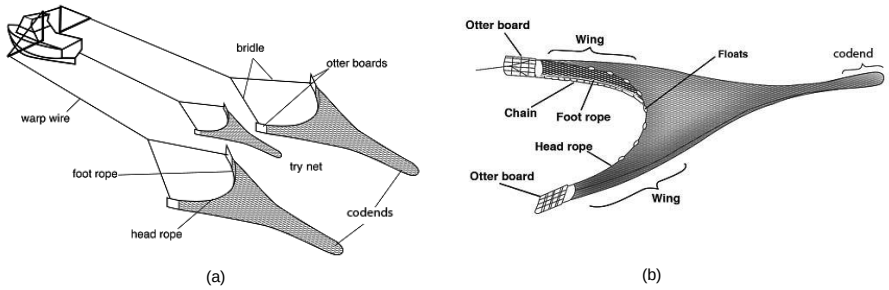


Figure 2. Bottom otter-trawling. (a) Trawls are usually fished from two outriggers attached at either side of the vessel. Additionally, a small try net might be deployed from the stern of the vessel to assess shrimp densities before and during trawling. (b) A bottom otter-trawl is a cone-shaped net consisting of a body which is closed by a codend and with lateral wings extending forward from the opening. The otter trawl is kept open horizontally by two otter boards (source: Gillett, 2008).

Bottom otter-trawling (Fig.2) is the most common method to fish for shrimp. Although it is very efficient, it is also a 'catch-all' technique. The poor selectivity of the small-meshed nets produces very high amounts of bycatch, particularly in tropical areas. This bycatch mainly consists of small and low-value 'trash fish' and invertebrates, which are discarded (Andrew and Pepperell, 1992). Shrimp trawl fisheries are the world champion in discards, accounting for 27% (1.86 million tons) of the estimated total discards from global fishing activity (Kelleher, 2005). On average, it is estimated that shrimp

trawling produces bycatch-to-shrimp ratios of 5:1 in temperate and sub-tropical waters, and 10:1 in tropical waters (Ye et al., 2000; EJF, 2003), but as much as 40 kg of bycatch for each kg of shrimp is no exception in certain tropical shrimp fisheries (Andrew and Pepperell, 1992).

Bycatch, particularly when discarded, is a serious concern for a number of reasons. First, the lack of identification and registration of discarded fauna, including vulnerable and threatened species such as sharks, rays and sea turtles, impedes a proper assessment of their status and trends, hampering management. Second, bycatch in one fishery might constitute target catch for other fisheries in the same area, creating interactions among fleets that complicate management. Third, bycatch, like target catch, affects the overall structure of trophic webs and living habitats. Finally, discarding animals who do not survive the catching process raises the ethical issue of wastage of natural production (Gillett, 2008).

The issues related to bycatch in tropical shrimp trawling largely relate to the three aspects to be included in an EAF. As outlined earlier (section 1.2), these include (1) trophic relationships, (2) competition between fleets and (3) impacts on habitats and species communities (Pauly and Chuenpagdee, 2002). While many shrimp fisheries were traditionally managed using single-species stock assessment models, the application of an EAF in shrimp trawling essentially needs to address ecological and socio-economic problems associated with bycatch (Gillett, 2008). Nevertheless, the food web related impact of removal of the target species, and effects of trawling on seabed habitats remain major concerns as well (EJF, 2003).

2.2 THE ATLANTIC SEABOB SHRIMP

Atlantic seabob *Xiphopenaeus kroyeri* (Crustacea: Penaeidae) (Heller, 1862) is a rather small penaeid shrimp (Fig. 3, Fig 4.), widely distributed in the Western Atlantic, from North Carolina (USA) through the Gulf of Mexico and Caribbean Sea to Southern Brazil (Holthuis, 1980) (Fig. 5). Adult *X. kroyeri* populations live in estuarine and shallow nearshore waters, characterized by fine substrates (Costa et al., 2007; Freire et al., 2011). This in contrast to other penaeid shrimps in the Western Atlantic (mainly *Penaeus sp.*), which are typically found further offshore (Villegas and Dragovich, 1984). Juvenile *X. kroyeri* prefer brackish waters, nursing in estuarine or inshore coastal waters. Adults move further offshore to spawn and planktonic larvae migrate back to the nursery grounds (Dall et al., 1990; Castro et al., 2005) (Fig. 3). In southern Brazil, recruitment of *X. kroyeri* was found to occur year-round, but with varying intensity (Branco et al., 1999; Castro et al., 2005; Branco, 2005; Almeida et al., 2012). *Xiphopenaeus kroyeri* is a fast growing species, reaching total lengths above 10 cm (Holthuis, 1980), with females being significantly larger than males (Branco et al., 1994). Life span shows sexual dimorphism,

averaging 21 months for females versus 16 months for males (Heckler et al., 2013b). Recent phylogenetic research has revealed that *X. kroyeri* is not a single species, but includes several cryptic (sub)species (Gusmao et al., 2006; Gusmao et al., 2013). Their geographic occurrence, and potential differences in ecology or morphology remain to be revealed.

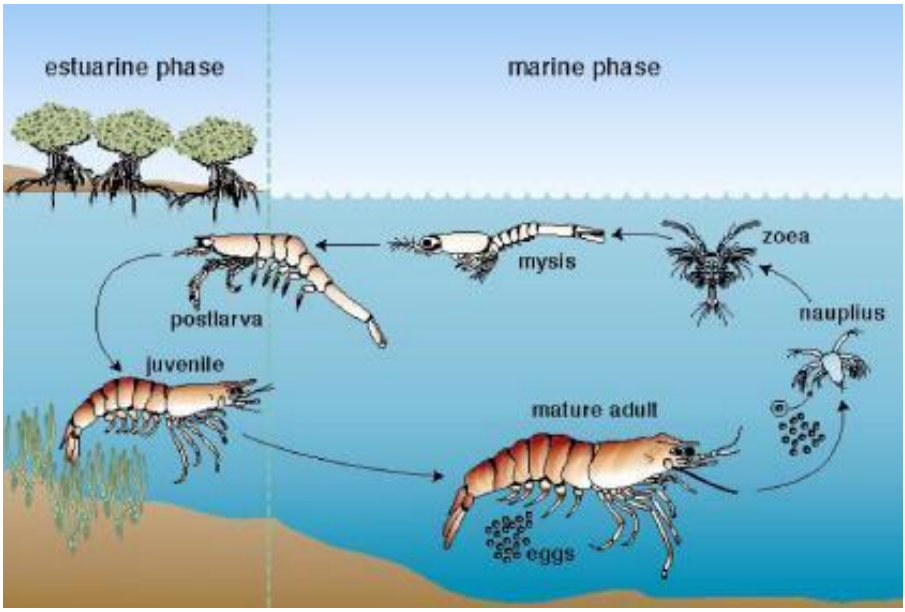


Figure 3. Life cycle of a penaeid shrimp (after Crocos and Kerr, 1983)

Xiphopenaeus kroyeri can be very abundant, and locally constitutes the single dominant epifaunal organism up to ca. 30 m depth (e.g. Guéguen, 2000a). This makes it an accessible resource for coastal fisheries, being one of the main target species for artisanal fisheries in southern Brazil (Branco, 2005; Silva et al., 2013). In recent decades, commercial shrimp trawling has shown increasing interest in *X. kroyeri*, in response to the overexploitation of *Penaeus sp*. stocks further offshore (e.g. Chin-A-Lin and IJspol, 2000). This caused a considerable increase in global landings of *X. kroyeri* from ca. 11,000 tons in 1990 to nearly 50,000 tons in 2013, making it one of the top ten most caught penaeid shrimps in the world (Silva et al., 2013; FAO, 2014a).

Figure 4. Atlantic seabob shrimp *Xiphopenaeus kroyeri* caught off Suriname

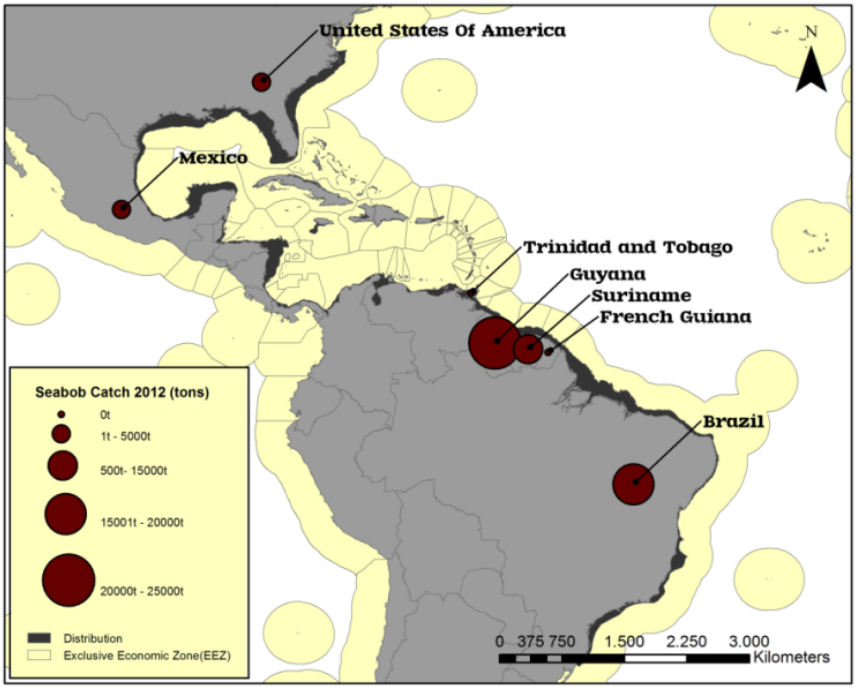


Figure 5. Distribution of the seabob shrimp *Xiphopenaeus kroyeri* along the coasts of the Americas (dark grey) and landings of seabob per country. (Adapted from FAO, 2014a by Torrez, 2015)

Most studies on *X. kroyeri* have been done in Brazil, where seabob shrimp landings are historically highest (FAO, 2014a), including research on the species' ecology (e.g. Costa et al., 2007; Castilho et al., 2008; Simoes et al., 2010), reproductive biology (e.g. Heckler et al., 2013a; Castilho et al., 2015), population dynamics (e.g. Castro et al., 2005; Heckler et al., 2013b), and population genetics (Gusmao et al., 2006; Gusmao et al., 2013). Given the wide latitudinal range in which *X. kroyeri* occurs, associated with a variety of environmental conditions, these findings may not be applicable to all populations of the species. Indeed, biological and morphological parameters, reproductive periods and spatio-temporal distribution of *X. kroyeri* differ between the regions studied (e.g. Oliveira, 1991; Castro et al., 2005; Fernandes et al., 2011; Almeida et al., 2012; Heckler et al., 2013a). While Guyana and Suriname currently account for a major part of the global landings (Fig. 5), research on *X. kroyeri* along the northern coast of South America remains very limited. The importance of *X. kroyeri* in benthic communities and its role in marine food webs therefore remains largely unknown in this area.

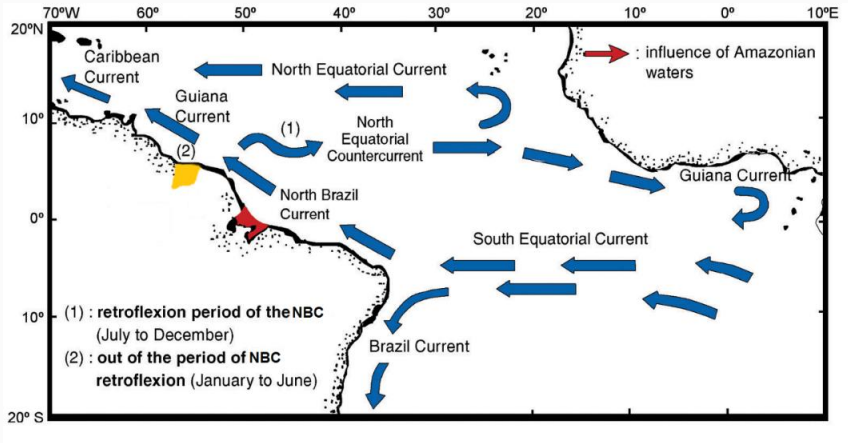
2.3 SEABOB FISHERIES IN SURINAME

Suriname is situated along the northern coast of South America, bordered by the Atlantic Ocean in the north, Guyana to the west, Brazil to the south and French Guiana to the east. Together with its neighboring countries Guyana and French Guiana, the region is referred to as the Guianas. Conditions on the Suriname continental shelf are profoundly shaped and influenced by discharge from the Amazon River (see Box 4 for more information on the abiotic characteristics of the inner Suriname Shelf).

Suriname has a population of approximately 500,000, 85% of whom live near the coastline, where >5000 people are employed directly in marine fisheries (FAO, 2008). Seabob shrimp is one of the most important fishery resources in Suriname, targeted by both artisanal and industrial fishing fleets. With landings of 8,000 to 10,000 tons per year, Suriname is the country with the third highest production of Atlantic seabob shrimp in the world (FAO, 2014a). About one-tenth of the landings is generated by ca. 500 artisanal fishermen who seasonally target *X. kroyeri* using fyke nets in river estuaries, and sell their catch fresh or dried on the local market (LVV, 2010). Main catches of the species are done by shrimp trawlers further offshore, and the term 'seabob fisheries' in the rest of this thesis refers to the offshore trawling fleet. Seabob trawlers started operating off the coast of Suriname in 1996, and their catches are exported frozen to markets in Europe and (a minority) in the US (J. Jagroop & F. Heimans, pers. comm). Half of the Suriname seabob trawling fleet is foreign-owned, as part of the Dutch shrimp company Heiploeg Group. The other half is operated by the Surinamese fishing company SAIL (LVV, 2010).

BOX 4. THE INNER SURINAME SHELF

The inner part of the Suriname Exclusive Economic Zone (EEZ) is characterized by a wide and gently sloping continental shelf, which is part of the Guianan Ecoregion of the North Brazil Shelf Province (Spalding et al., 2007). Beyond the 100 m isobath, water depth rapidly increases to 4600 m as the Suriname Shelf plunges into the depths of the Western Central Atlantic Basin. The Suriname EEZ is profoundly influenced by the turbid freshwater discharge from the Amazon River (Heileman, 2008), discharging on average 5330 km3 freshwater into the Atlantic Ocean each year (Dai and Trenberth, 2002). The water from the Amazon is carried northwest by the North Brazil Current and the Guiana Current (Johns et al., 1998; Hellweger and Gordon, 2002).



The waters off Suriname (in yellow) are profoundly influenced by freshwater discharge from the Amazon estuary (in red), which is carried northwest by the North Brazil Current (NBC) and its extension, the Guiana Current. The NBC seasonally reflects into the North Equatorial Countercurrent (adapted from Artigas et al., 2003).

The shelf waters of the Guianen Ecoregion can be characterized by three major zones parallel to the coast (Lowe-McConnell, 1962; Cadée G.C., 1975). The brown nearshore waters have a high turbidity and low salinity due to suspension of the muddy deposits and freshwater input of both the Amazon and local rivers. Between 20 and 50 km offshore, the combination of riverine nutrient input and decreased turbidity creates a productive zone with high chlorophyll concentrations, termed the green water zone. Offshore from this zone transparancy further increases, while nutrients become limited for primary production, causing blue waters. Blue waters cover most of the EEZ and receive nutrients from upwelling along the continental slope (Artigas et al., 2003).

BOX 4. (CONTINUED)

Sea surface temperatures are around 27-29°C throughout the year, and wind and wave patterns in the area are dominated by north-eastern trade winds (Miloslavich et al., 2011)Most rainfall, and thus peak river discharge, occurs between December and July (Amatali, 1993, Hu et al., 2004). From August to November, the GC weakens due to retroflection of the NBC into the North Equatorial Counter Current (NECC). This causes drier and calmer weather in the second half of the year, with warmer sea surface waters (Amatali, 1993; Augustinus, 2004).

Brown and green waters meet some 20 km off the coast of Suriname

The Suriname seabob fleet consists of 22 licensed vessels, typically 'Florida-type' outrigger trawlers (Fig. 6) with an overall length of 20 to 25 m and a maximum engine power of 500 hp (Southall et al., 2011). The vessels are equipped for twin-rig bottom-trawling, which involves dragging two trawls attached to two steel-footed wooden doors and a sledge at either side of the vessel, resulting in two port- and two starboard-codends (and therefore also referred to as quad-rig trawling) (Fig. 6). Mesh size of each trawl is 57 mm in the body and wings of the trawl and 45 mm in the codend. Each trawl is obligatory equipped with a Turtle Excluder Device (TED) and a Bycatch Reduction Device (BRD) (see further). In addition to the main trawls, a small try net is deployed from the stern of the vessel to quickly assess shrimp densities both before and during fishing (Southall et al., 2011) (Fig. 6).

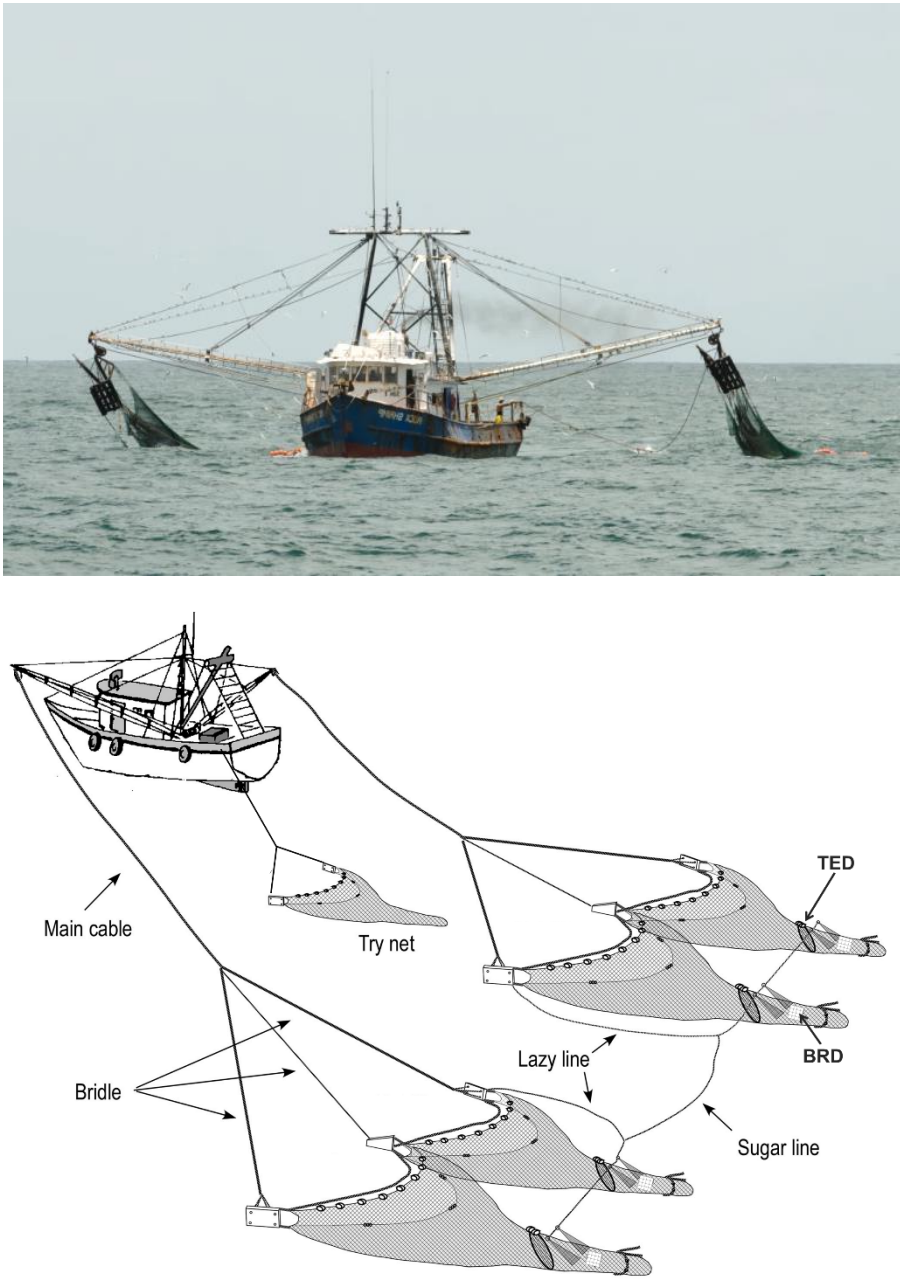


Figure 6. (Top) A typical 'Florida type' outrigger seabob trawler off Suriname; (Bottom) Net configuration in the Suriname seabob fleet: twin-rig otter trawls fished from outriggers and a try-net deployed from the stern. TED = Turtle Excluder Device, BRD = Bycatch Reduction Device (See further) (Adapted from Scott-Denton et al., 2010).

2.4 STEPS TOWARDS SUSTAINABLE SEABOB FISHERIES IN SURINAME

The environmental problems associated with wild-caught tropical shrimp have caused them to be considered an unsustainable seafood product. This is now widely recognized, with tropical shrimp scoring very low in seafood sustainability guides that are increasingly used by consumers worldwide, especially in Western countries where most tropical shrimp are consumed (EJF, 2003). As a response to European market demand for sustainable seafood products, and in reaction to the negative perception of wild-caught tropical shrimp, Heiploeg Group, together with SAIL, took the initiative in 2007 to improve the catch process in the Suriname seabob trawling fleet (Sanders and Meskens, 2010).

This initiative was welcomed and supported by the Suriname Fisheries Department, for two main reasons. First, seabob trawling had been controversial since the start, because the industrial fishery raised concerns among artisanal fishermen. Artisanal gillnetters feared that seabob trawling would deplete an important food source for their target catch, demersal fishes, while artisanal seabob fishers were concerned for their shrimp catches (M. Lall and M. IJspol, pers. comm.). Second, the last decades have seen a great decline in the catches of larger penaeid shrimp (*Penaeus* sp.) off Suriname. Decreasing catch-per-unit efforts led to low profitability, causing a dramatic decrease in the numbers of *Penaeus* trawlers. Accordingly, *Penaeus* landings declined from ca. 4,000 tons at the end of the 1970s to less than 200 tons in 2008 (Fig. 7) (LVV, 2013). It was estimated that the loss of export value from marine shrimp for Suriname was ca. 15 million USD only for the period 2000-2010 (LVV, 2013). The collapse of the fishery for large penaeid shrimp, once by far the most important fishery sector in terms of value (Bansie R., 2010), made clear that even shrimp stocks can be overfished, and therefore need to be properly managed.

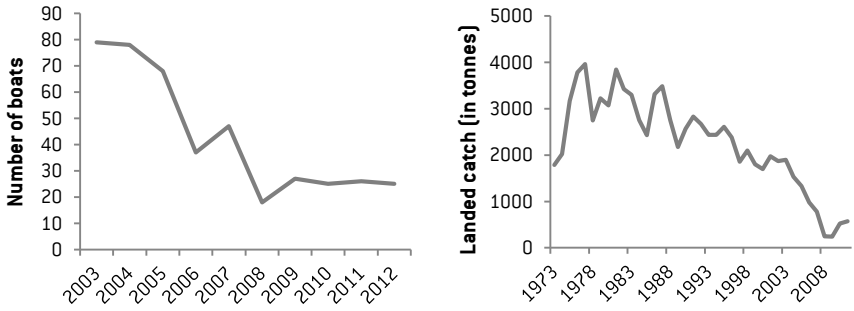


Figure 7. Collapse of the fishery for penaeid shrimp (Penaeus sp.) off Suriname. Declining profitability led to a steady decline in the number of boats (left) and landed catch (right) (source: LVV, 2013).

The improvement process in the Suriname seabob fishery started in 2007. While the number of fishing licenses was formerly around 30, it was agreed to maximally allow 22 vessels in the fishery. Improvements in data collecting practices included a more complete and regular reporting of the catches to the LVV fisheries ministry, and the initiation of random catch sampling to collect morphological data on the landed shrimp. These data allowed for formal assessment of the Suriname seabob stock, which was initiated at the annual scientific meeting of the Regional Caribbean Fisheries Mechanism (CRFM) in 2009 (CRFM, 2009). This stock-assessment led to the establishment of a Harvest Control Rule (HCR), which specifies the maximum fishing effort (in days-at-sea; DAS) in relation to the catch-per-unit-effort (CPUE) (Fig. 8). In the current HCR, the target CPUE is set at 1.65 t/day to achieve optimal sustainable yields. Fishing effort should be reduced if CPUE falls below the trigger point of 1.48 t/day, and fishing should completely stop when the CPUE reaches the limit of 0.89 t/day.

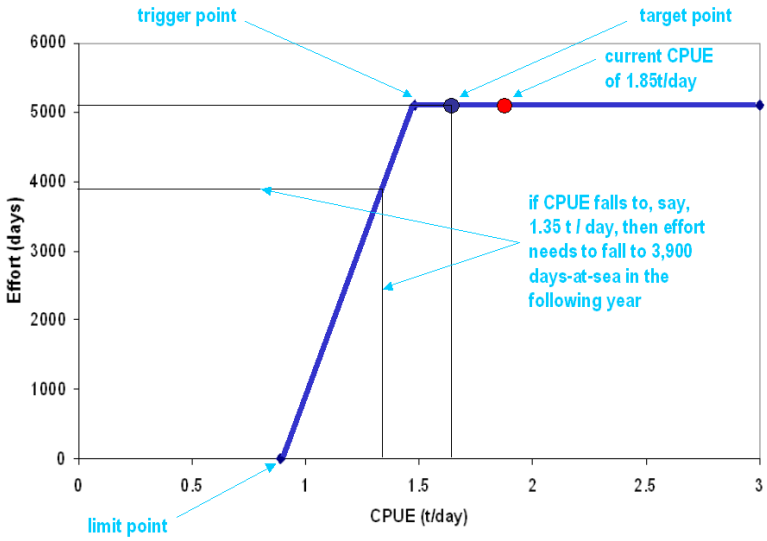


Figure 8. The seabob Harvest Control Rule (HCR) specifies the maximum allowable fishing effort (in day-at-sea) for a given catch-per-unit-effort (CPUE) (source: LVV, 2010).

Another important step in the improvement process was the delineation of the legal seabob trawling zone. Within Suriname's territorial waters (Exclusive Economic Zone; EEZ), stretching 370 km (200 nautical miles) offshore from the 386 km long coastline, the operation of seabob trawlers is spatially restricted to the area delimited by lines nominal to the 10 and 15 fathoms water depth (resp. 18 and 27 m), extending to 18 fathoms (33 m) in the eastern part of the EEZ (Fig. 9). The waters inshore of the 10 fathom line are reserved for artisanal fisheries, which – besides targeting seabob shrimp - mainly target demersal fishes with gillnets, operated from wooden, open or decked

'Guyana-type' boats (Bhagwandin, 2012). The artisanal fleet is by far the most important fishing sector in Suriname, generating the most employment, and representing about 70% of the country's fishery landings (Bhagwandin, 2012). In the deeper waters of the EEZ, beyond 15 – 18 fathoms, fish trawlers, shrimp-trawlers (targeting larger penaeid shrimp species) and longliners operate (Fig. 9) (LVV, 2013).

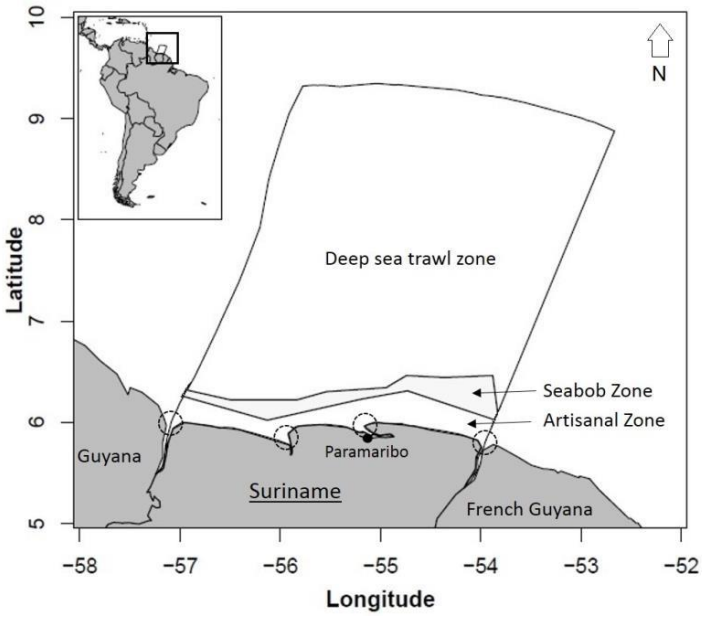


Figure 9. The Suriname Exclusive Economic Zone (EEZ) with indication of the legal zonation for fisheries: artisanal, seabob and deep sea trawl zone. The four major estuaries along the Suriname coast are marked with open circles: from West to East the Corantijn-Nickerie estuary, the Coppename-Saramacca estuary, the Suriname-Commewijne estuary and the Marowijne estuary.

Compliance with the depth restrictions to trawl fisheries is controlled through a Vessel Monitoring System (VMS). All (semi-) industrial vessels have a VMS in place since 2008, and efforts are now being made to equip the artisanal fleet with a VMS as well (M. IJspol, pers. comm). The VMS sends real-time information on vessel speed (to distinguish trawling from steaming), position and direction to the Fisheries Department of the Suriname Ministry of Agriculture, Livestock and Fisheries (LVV), which tracks all vessels' movements. When analysed correctly, VMS data also reveal the spatial distribution of fishing effort. Within the legal fishing zone, seabob trawling effort is not equally distributed, but occurs mainly at certain 'hot spots' of fishing activity (Fig. 10) (Pérez, 2014).

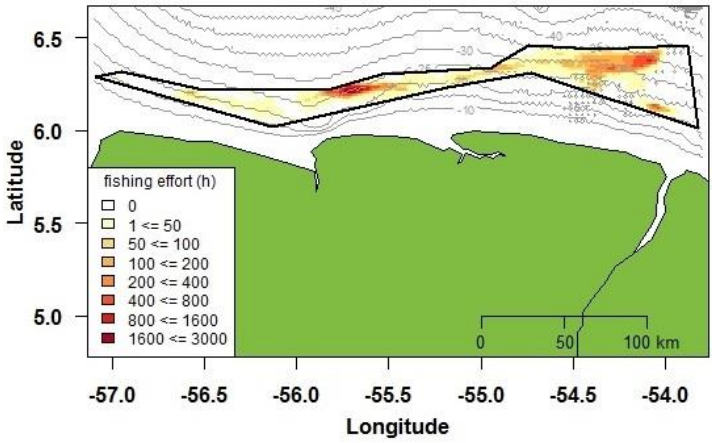


Figure 10. Map of the inner Suriname Shelf showing aggregated fishing effort (in hours) of the seabob trawling fleet over the period 2007-2013, illustrated here for the main rainy season (generally March - July). The black polygon delineates the legal seabob trawling area and bathymetric lines indicate 5 m depth increases starting from 10 m isobath (source: Pérez, 2014).

Further, each trawl is mandatorily equipped with a Turtle Excluder Device (TED) and a Bycatch Reduction Device (BRD) (Fig. 11). The aluminum TED is a so-called 'super shooter', with a bar spacing of 10 cm and installed in a downward-excluding configuration. Each codend is also fitted with a square-mesh-panel BRD (11 x 11 meshes, 15 cm stretched mesh size), inserted ca. 40 cm behind the TED in the upper side of the codend. While TEDs have been in place since 1999, BRDs were made obligatory in 2009 to reduce bycatch of small finfish (LVV, 2010).

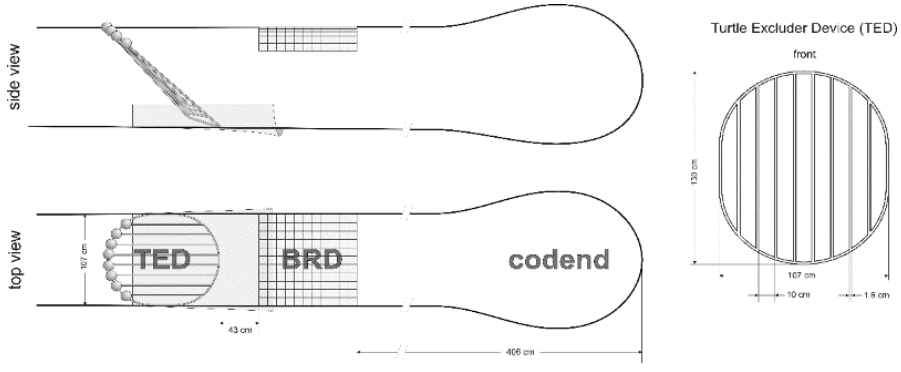


Figure 11. Details of a trawl codend with Turtle Excluder Device (TED) and square-mesh panel Bycatch Reduction Device (BRD) ©Hans Hillewaert/ILVO.

Finally, to ensure a proper implementation of management measures for the Suriname seabob fishery, a stakeholder platform was set up: the Seabob Working Group (SWG). The SWG gathers monthly, bringing together representatives from the fishing industry, the artisanal seabob fleet, the LVV Fisheries Department and NGOs (e.g. the World Wildlife Fund; WWF). At each SWG meeting, figures on the CPUE of the seabob trawling fleet are discussed and compared against the HCR, and other issues in the fishery are discussed (Southall et al., 2011). Because the CPUE has been fairly constant (Fig. 12), no major interventions in allowable fishing effort have been applied in recent years (M. IJspol, pers. comm.). All management restriction and license conditions that apply to the seabob trawling fleet in Suriname are stipulated in a legally binding management plan for the fishery (LVV, 2010).

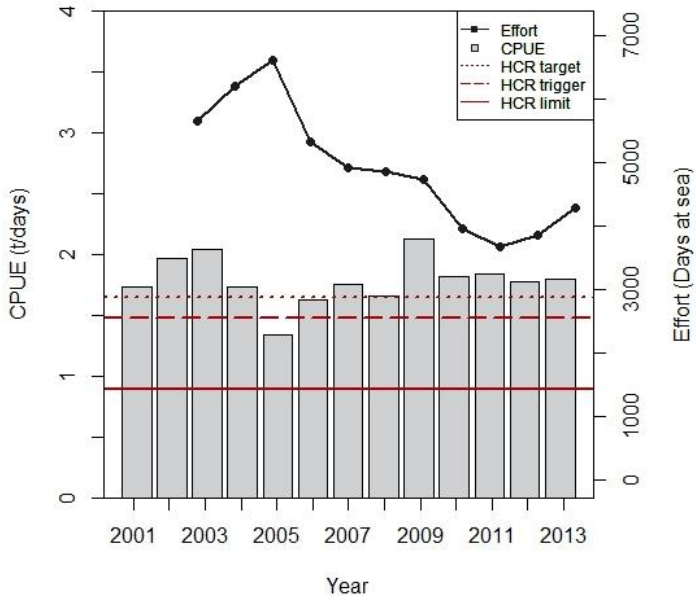


Figure 12. Fishing effort and CPUE of the Suriname seabob trawling fleet for the period 2001-2013, with indication of the HCR target, trigger and limit CPUE values (Source: Pérez, 2014)

In 2010, after a pre-assessment in 2009, the Suriname seabob fishery entered into full assessment against the Marine Stewardship Council (MSC) principles and criteria for Sustainable Fisheries. The assessment was successful and the certificate was granted in November 2011 (Southall et al., 2011), making the Suriname seabob fishery the first tropical shrimp fishery in the world to obtain this ecolabel. While the overall score of the fishery was sufficient for MSC certification, several individual Performance Indicators of the MSC standard did not meet the minimum required score of 80. These were set as conditions which the fishery has to address for continued certification (Southall et al., 2011) (Box 5).

BOX 5. MARINE STEWARDSHIP COUNCIL (MSC) CERTIFICATION OF THE SURINAME ATLANTIC SEABOB SHRIMP FISHERY

As of November 2011, the Suriname Atlantic seabob shrimp fishery was certified according to the Marine Stewardship Council Principles and Criteria for Sustainable Fisheries. The fishery obtained an overall score of 80 or more against each of the MSC principles:

Principle 1: **Sustainability of Exploited Stock** (Score = 84.4)
Principle 2: **Maintenance of Ecosystem** (Score = 80)
Principle 3: **Effective Management System** (Score = 80.6)

The fishery attained a score below 80 against a number of individual Performance Indicators (PIs). Therefore, six conditions were set upon MSC certification, which should be addressed (i.e. improve performance to at least score 80) within the lifetime of the certificate (5 years).

Condition 1. Good Information on all other fishery removals from the stock
PI 1.2.3 – Information / monitoring: Relevant information is collected to support the harvest strategy

Condition 2. Ensure main bycatch species are within biologically based limits
PI 2.2.1 – Status: The fishery does not pose a risk of serious or irreversible harm to the bycatch species or species groups and does not hinder recovery of depleted bycatch species or species groups.

Condition 3 Nature, distribution and vulnerability of main seabed habitats
PI 2.4.3 – Information / Monitoring: Information is adequate to determine the risk posed to habitat types by the fishery and the effectiveness of the strategy to manage impacts on habitat types.

Condition 4. Main functions of the components of the ecosystem are known
PI 2.5.3 – Information / Monitoring: There is inadequate knowledge of the role of seabob within the ecosystem. The role that climatic and oceanographic events and patterns, as well as anthropogenic activities may have on the ecosystem are also not well understood.

Condition 5. Explanations for management action
PI 3.2.2 – Decision-making processes: The fishery-specific management system includes effective decision-making processes that result in measures and strategies to achieve the objectives.

Condition 6. Consistent application of sanctions to deal with non-compliance
PI 3.2.3 – Compliance and enforcement: Monitoring, control and surveillance mechanisms ensure the fishery's management measures are enforced and complied with.

Source: Southall et al., 2011

While three conditions related to either the target species (Condition 1) or the management system (Condition 5 & 6), 3 of the 6 conditions concerned the conservation of the ecosystem in which the fishery operates (Box 5). More specifically, the MSC public certification report (Southall et al., 2011) states that:

- the fishery should demonstrate that bycaught ray species are within biologically-based limits or develop strategies that will mitigate against impacts of the fishery on rays and other vulnerable species (Condition 2);

- an appropriate and precautionary approach to managing the fisheries potential to impact seabed habitats should be informed by data on the nature and distribution of the main seabed habitats occurring in the area where the seabob fishery takes place (Condition 3);

- targeted investigations should be carried out that seek to enhance understanding the role of seabob in the ecosystem in order to facilitate further research into the effects of the fishery on the target stock and the implications of this for other species and overall food web dynamics (Condition 4).

These three conditions all relate to impacts of the fishery on the structure and functioning on the coastal ecosystem in Suriname, which could not be properly evaluated during the MSC assessment due to a lack of information (Box 6). The conditions highlighted the need for bio-environmental research on the Suriname Shelf and the assessment of ecosystem impacts of seabob trawling.

BOX 6. NORTH – SOUTH COOPERATION

Since the research was executed in Suriname, a partner country in the VLIR-UOS programme, this thesis has a clear north-south component. A unique partnership was established, between Ghent University and ILVO in Belgium, and Adek University and the LVV fisheries ministry in Suriname. This was made possible through the network and funding of VLIRUOS, and with the logistic support of the fishing company Heiploeg Suriname. The research and activities within this PhD have contributed to two issues which afflict Suriname but with a broader developmental relevance as well.

(1) While the seabob fishery was mainly triggered for improvements by the demand for certified sustainable seafood at the European market, there is clear local need for sustainable fisheries management in Suriname. In Suriname, 85% of the population lives near the coastline, where over 5000 people (ca. 1% of the population) is employed directly in marine fisheries (FAO, 2008). As seen in many developing world countries, fisheries are an important economic activity in the coastal area, where alternative sources of employment might be scarce or cannot guarantee basic livelihood. As such, they play a crucial role in income generation and poverty alleviation (e.g. Mathew, 2003). To avoid negative socio-economic consequences of overexploitation (e.g. collapse of *Penaeus sp.* shrimp fisheries, see above), sustainable management of Suriname's fisheries resources, including the seabob shrimp, is crucial.

(2) The need for fisheries management in Suriname is in sharp contrast to a shortage of local capacity in fisheries science. Marine research and education in Suriname is currently almost non-existent, hampering effective training of students and staff. Due to the close cooperation with Adek University during this PhD study, marine research and training have revived among students and staff of Adek University. Local university staff and students were involved in the project, assisting the fieldwork, sample processing, or as their own master or bachelor thesis project (e.g. Landburg, 2013).

In cooperation with Adekus, LVV and WWF, two educational posters were produced on the common marine fishes and invertebrates occurring off the Guianas (Annex 1.2, 1.3).

Students of Adek University (Bachelor Environmental Sciences) assisting in processing of water samples near the Marowijne Estuary.

BOX 7. MARINE BIOLOGICAL RESEARCH IN SURINAME

Since the mid-20th century, the Suriname Shelf has been increasingly studied, mostly through scientific expeditions led by the Dutch Navy. These cruises included research on the bathymetry, hydrography, oceanography, geology and biology of the waters off Suriname (Geijskes, 1968). The biological research focused mainly on the collection of specimens, resulting in taxonomic information on species distributions, and descriptions of new species (e.g. Holthuis, 1959; Walenkamp J.H.C., 1976; Logan, 1990).

After 1975, marine biological research on the Suriname Shelf has been very limited, and mainly included fisheries-related trawl surveys (e.g. Aizawa et al., 1983; Bianchi, 1992a; Charlier and Babb-Echteld, 1994a), and environmental impact assessments for oil exploration (e.g. ESC, 2011). These studies have revealed a general inshore-offshore zonation of the benthic communities on the Suriname Shelf, as also observed in neighboring Guyana (Lowe-McConnell, 1962) and French Guiana (e.g. Durand, 1959; Guéguen, 2000a).

Nevertheless, while the abiotic processes shaping the structure of the Suriname coast and inner continental shelf are now relatively well understood (e.g. Augustinus, 1978; Eisma et al., 1991; Augustinus, 2004), knowledge on the structure and functioning of the marine ecosystem of Suriname is still limited, and detailed information on the ecological distribution and structure of benthic species communities and habitats is largely lacking.

Between 1952 and 1973, the A902 *Hr. Ms. Luymes* of the Royal Dutch Navy undertook several scientific expeditions in Suriname's territorial waters. Since the country's independence from The Netherlands in 1975, marine research off the coast of Suriname has been limited. (Source: www.onzevloot.weebly.com/)

3 AIM AND OBJECTIVES

In recent years, seabob shrimp (*Xiphopenaeus kroyeri*) fisheries off Suriname have undergone important improvements in management, and have started to adopt an ecosystem approach to fisheries management. Nevertheless, as highlighted during the MSC assessments, crucial information is lacking to assess the impact of seabob fisheries on certain aspects of the regional ecosystem structure and functioning.

Therefore, **the overall aim of this study is to provide relevant knowledge needed for the development of an improved ecosystem based approach to the management of *Xiphopenaeus kroyeri* trawl fisheries off Suriname.**

To achieve this, four main **objectives** were defined:

1) to characterize the benthic assemblages and habitats of the inner continental shelf where *X. kroyeri* fisheries take place (ecosystem structure)

2) to study the role of *X. kroyeri* in the coastal food web of Suriname (ecosystem functioning)

3) to assess the impact of *X. kroyeri* trawling on ecosystem structure and functioning (ecosystem impact)

4) to define recommendations for an ecosystem approach to the seabob fisheries management in Suriname (management implications)

So far, the research in the framework of the MSC label for seabob fisheries in Suriname has focused on the stock of *X. kroyeri*, leading to a stock assessment model and a Harvest Control Rule (HCR). However, an EAF essentially recognizes that fisheries affect ecosystem structure and functioning. Given the lack of bio-environmental research on the Suriname Shelf, the first and second objective relate to the characterization of structural and functional ecosystem aspects, respectively (Fig. 13). The focus of the third objective is on structural impacts of fishing, by studying bycatch in the seabob fishery. Within the timeframe of this doctoral thesis, it was not feasible to use an ecosystem modelling approach to fully quantify the effects of seabob fisheries on the functioning of the benthic Suriname ecosystem. This therefore stands out as a priority for further research. For the fourth objective, all scientific results are discussed in a management context and the scientific findings of the first three objectives are translated into management recommendations to allow for a sound EAF application in the Suriname seabob fishery.

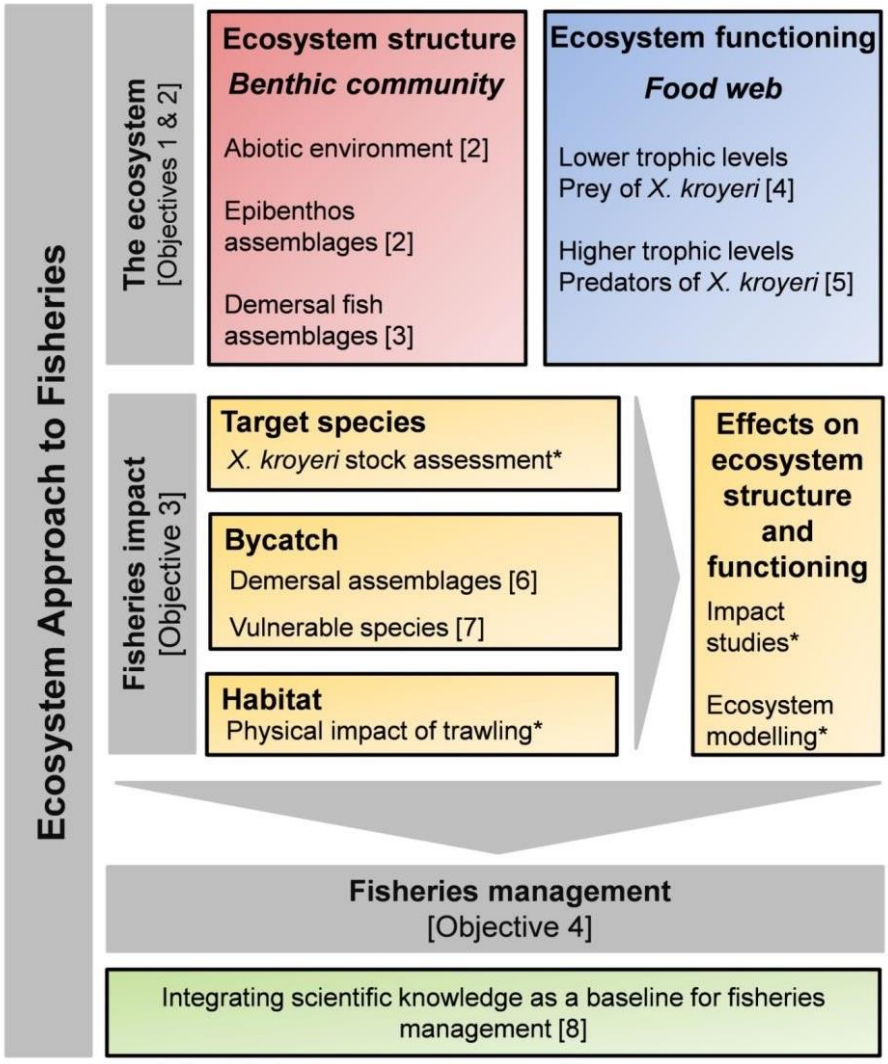


Figure 13. Theoretical framework of this doctoral thesis. Structural (Objective 1) and functional (Objective 2) ecosystem features are studied, and the way they are impacted by fisheries (Objective 3). The resulting information is discussed in a management context (Objective 4). Numbers between brackets denote the respective chapters in which the different topics are addressed. Aspects not included in this thesis are marked with an asterisk (*).

BOX 8. FISHERMEN'S SCIENCE

The research conducted in this thesis involved extensive data collection at sea. Since Suriname has no marine research vessel, agreements were made with the seabob fishing company Heiploeg Suriname which assigned a vessel and crew to assist in the research. The trawler *Neptune-6* was equipped for our research purposes with a modified try-net, 110V A/C current, a sample freezer and an extra davit at the stern for deployment of a Van Veen grab, hyperbenthic sledge, CTD-profiler and Niskin-bottle. Although most research trips also involved commercial fishing, catches were generally lower than on a normal fishing trip. Because the salary of captain and crew depends on the amount of landed catch, the loss of income resulting from research activities was compensated by the company, guaranteeing the income of the fishermen. This was crucial to obtain full cooperation of the captain and crew, whose help was essential in every stage of the fieldwork. They assisted in deploying the sample equipment, processing the samples, identifying the species, measuring of fish and recording of data. While the researcher joined most cruises, the last four research trips of the 2012-2013 trawl survey were conducted by the fishermen themselves, assisted by sea-going observers from LVV fisheries ministry. The accuracy of the data collected during these trips was assured by the experience of the captain, crew and observers gained during previous research trips, and through a detailed sampling protocol that was provided, together with species identification guides (Annex 1.3). Further, mutual trust existed between the researcher and the fishermen, which is crucial for this kind of 'fishermen's science' to yield reliable scientific information (e.g. Conway and Pomeroy, 2006). Insights on the fishery and the ecosystem were also gained through day-to-day interactions with the fishermen and sea-going observers. Although no formal interviews or questionnaires were done to quantify this local ecological knowledge, reference to this information is made throughout the thesis as 'personal communication'. Clearly, the cooperation with fishermen was essential for this research project. Moreover, fishermen's participation in the research is likely to benefit future management of the fishery. Involving fishermen in data collection creates ownership of the results, and a better understanding of management measures resulting from new research insights (e.g. Prince et al., 2015)

Fishermen assisting in data recording on board Neptune-6

4 OUTLINE OF THE THESIS

Apart from the general introduction and the general discussion, this thesis is a compilation of research articles (published, currently under revision or in preparation). The content of each chapter resembles almost exactly the published or submitted papers. Each chapter is therefore intended to be an autonomous part, which can be read separately from the other chapters. Inevitably, there is some overlap between the introductions and material and methods sections of the different chapters. Cited literature is compiled in a single list at the end of the thesis. In congruence with the four objectives of this PhD study, the thesis contains four main parts, each one comprising one or two chapters.

In **PART I** of this thesis**,** we aimed to characterize the **demersal assemblages in the coastal waters of Suriname (objective 1).** The abiotic characteristics of the inner Suriname Shelf and the spatio-temporal distribution of epibenthic assemblages are described in **Chapter 2** (Willems et al., 2015b), based on an extensive trawl survey conducted in 2012. From the same trawl survey, data on the occurrence and distribution of the demersal fish fauna is reported separately in **Chapter 3** (Willems et al., 2015a) (Fig. 12).

Whereas the first part considers structural ecosystem features, **PART II** deals with functional ecosystem aspects, assessing **the role of *Xiphopenaeus kroyeri* in the coastal food web of Suriname (objective 2).** In **Chapter 4** (Willems et al. submitted a), the trophic ecology of *X. kroyeri* is investigated in order to identify the energy and carbon sources supporting this commercially important species. Next, in order to assess its overall importance in the food web, we looked at the contribution of *X. kroyeri* to the diet of demersal fishes in **Chapter 5** (Willems et al. submitted b).

PART III aimed to assess **the impact of *Xiphopenaeus kroyeri* trawl fisheries on the coastal ecosystem of Suriname (objective 3)**. As such, **Chapter 6** (Willems et al. In Prep.) focuses on the general impact of fishing on demersal assemblages by investigating the catch composition during commercial seabob trawl fisheries off Suriname. As a species group of particular conservation concern, **Chapter 7** focuses on the bycatch of rays, addressing the effectiveness of the current fishing gear adaptations in mitigating ray bycatch (Willems et al., 2016).

Finally, **PART IV** translates scientific knowledge into management recommendations **(objective 4)**, in order to move **towards sustainable management of *Xiphopenaeus kroyeri* fisheries in Suriname. Chapter 8**, the general discussion, presents a framework on how to move from science to policy, and to use the information gathered in this doctoral thesis for further

implementation of an Ecosystem Approach to Fisheries management in Suriname (Fig. 12).

PART I

DEMERSAL ASSEMBLAGES IN THE COASTAL WATERS OF SURINAME

2

SPATIO-TEMPORAL DISTRIBUTION PATTERNS OF THE EPIBENTHIC COMMUNITY IN THE COASTAL WATERS OF SURINAME

Modified from:

Willems, T., De Backer, A., Vincx, M., Hostens, K., 2015. Spatio-temporal distribution patterns of the epibenthic community in the coastal waters of Suriname. Continental Shelf Research 108, 25-40.

This study aimed to characterize the spatio-temporal patterns of the epibenthic community in the coastal waters of Suriname. Data were collected on a (bi)monthly basis in 2012-2013 at 15 locations in the shallow (<40 m) coastal area, revealing three spatially distinct species assemblages, related to clear gradients in some environmental parameters. A species-poor coastal assemblage was discerned within the muddy, turbid-water zone (6 to 20 m depth), dominated by Atlantic seabob shrimp Xiphopenaeus kroyeri *(Crustacea: Penaeoidea). Near the 30 m isobath, sediments were much coarser (median grain size on average 345 ± 103 µm vs. 128 ± 53 µm in the coastal assemblage) and water transparency was much higher (on average 7.6 ± 3.5 m vs. 2.4 ± 2.1 m in the coastal assemblage). In this zone, a diverse offshore assemblage was found, characterized by brittle stars (mainly* Ophioderma brevispina *and* Ophiolepis elegans*) and a variety of crabs, sea stars and hermit crabs. In between both zones, a transition assemblage was noted, with epibenthic species typically found in either the coastal or offshore assemblages, but mainly characterized by the absence of* X. kroyeri. *Although the epibenthic community was primarily structured in an on-offshore gradient related to depth, sediment grain size and sediment total organic carbon content, a longitudinal (west-east) gradient was apparent as well. The zones in the eastern part of the Suriname coastal system seemed to be more widely stretched along the on-offshore gradient. Although clear seasonal differences were observed in the environmental characteristics (e.g. dry vs. rainy season), this was not reflected in the epibenthic community structure.* Xiphopenaeus kroyeri *reached very high densities (up to 1383 ind.1000 m^{-2}) in the shallow coastal waters of Suriname. As* X. kroyeri *is increasingly exploited throughout its range, the current study provides the ecological context for its presence and abundance, which is crucial for an ecosystem approach and the sustainable management of this commercially important species and its habitat.*

1 INTRODUCTION

Continental shelves cover only about 7% of the seabed surface (Snelgrove, 1999), yet their significance in terms of marine biodiversity and ecosystem goods and services can hardly be overestimated. Biological production in shelf seas supports over 90% of global fish catches (Pauly et al., 2002). Other benefits of coastal and shelf ecosystems include the provision of nursery habitats for commercial species, coastal protection, water purification, carbon sequestration and tourism (Barbier et al., 2011). de Groot et al. (2012) estimated the global value of the ecosystem services provided by marine coastal biomes (coral reefs, coastal wetlands and coastal systems) to be >13 times higher than the value of all other marine and terrestrial biomes combined. Coastal and shelf ecosystems require proper management measures to assure sustainable use of their natural resources and to maintain their ecosystem services (Barbier et al., 2011). To develop effective conservation strategies, basic knowledge on the structure and functioning of the coastal ecosystem is pivotal (Reiss et al., 2010).

The present study was conducted on the continental shelf of Suriname in South-America, an area influenced by Amazon River runoff (Hellweger and Gordon, 2002), causing muddy coasts (Eisma et al., 1991) and productive shelf waters (Smith and Demaster, 1996). Suriname's coastal waters support extensive artisanal and industrial fisheries (Bhagwandin, 2012), and other economic activities (notably near-shore oil exploitation) are expected to develop in the near future. Benthic fauna is commonly used in monitoring programs to study the impact of anthropogenic activities and to assess the health of coastal systems (Bilyard, 1987). Up till now, the ecological knowledge on the benthic communities of the Suriname Shelf is limited. Some taxonomic studies have been conducted prior to 1975 (e.g. Holthuis, 1959; Logan, 1990), while later work mainly consisted of fisheries-related trawl surveys (e.g. Aizawa et al., 1983; Charlier and Babb-Echteld, 1994a). Quantitative ecological research on benthic communities thus far only comprised one study in the intertidal area (Swennen et al., 1982) and scattered information from environmental impact assessments for oil exploration (e.g. ESC, 2011). As such, this is the first study describing the benthic community structure along the inner continental shelf of Suriname.

Due to the unstable nature of mud deposits in the nearshore waters below 20 m depth (Eisma et al., 1991; Augustinus, 2004), densities of macrobenthic infauna are expected to be very low in the shallow parts of the Suriname Shelf (Aller and Aller, 1986; Aller and Aller, 2004). Therefore, we focused on the epibenthos living on and near the sea bottom, which is known to dominate the benthic fauna in tropical soft-bottom habitats (Alongi, 1989). Information on the epibenthos is relevant for fisheries management as well, as epibenthic species are either exploited directly (e.g. crabs and shrimps) or serve as primary food source for commercially important demersal fishes (e.g. Salini et al., 1994).

The aim of this study was to characterize the epibenthic communities in the shallow (<40 m) continental shelf of Suriname by gathering data on species composition, abundance, biomass and biodiversity, and to investigate the spatio-temporal distribution patterns in the epibenthic community in relation to some environmental factors.

2 MATERIALS AND METHODS

2.1 STUDY AREA

The study was conducted on the continental shelf of Suriname (54 – 57 °W, 6 – 7 °N, Fig. 1), part of the Guianan Ecoregion of the North Brazil Shelf, and situated between the estuarine outflows of the Amazon and Orinoco Rivers (Spalding et al., 2007). The area is characterized by wide, gently sloping continental shelves, macrotides and upwelling along the shelf edge, and is profoundly influenced by the freshwater discharge from the Amazon River (Heileman, 2008). The Amazon River discharges on average 5330 $km^3.yr^{-1}$ freshwater into the Atlantic Ocean (Dai and Trenberth, 2002), with peak flows around June and low flows around November (Lentz and Limeburner, 1995). Amazon water is carried northwest by the North Brazil Current (NBC; e.g. Johns et al., 1998) and continues along the Guiana coasts with the Guiana Current (GC; Hellweger and Gordon, 2002). Furthermore, the NBC typically deviates to the east for several months between July and December, feeding into the North-Equatorial Counter-Current (NECC) (Richardson et al., 1994). The NBC-retroflection causes a periodical reduction in the intensity of the GC (Hellweger and Gordon, 2002). Low discharge and weakening of the GC causes a reduced arrival of Amazon water to the coast of Suriname in the second half of the year.

Suriname has a humid-tropical climate, with mean temperatures between 26.2 and 28.2 °C, and an annual rainfall between 1450 and 3000 mm (Amatali, 1993). The climate is influenced by the Inter-Tropical Convergence Zone (ITCZ) which passes over the country twice a year, creating two major seasons. The dry season lasts from August to November and the rainy season from December to July, the latter interrupted by a drier period ("short dry season") in February - April. (Amatali, 1993). The seasonality in rainfall determines the amount of freshwater discharged into the coastal waters from four rivers (on average 152 km3.yr-1 in total, Amatali, 1993). These rivers enter the Suriname coast via estuaries and are, from Guyana to French Guyana (west to east), the Corantyne, Coppename, Suriname and Maroni rivers, respectively. Shelf waters in the region can generally be characterized by three major zones parallel to the coast (Lowe-McConnell, 1962; Cadée G.C., 1975; Smith and Demaster, 1996). The brown inshore waters have a high turbidity and low salinity due to suspension of the muddy deposits and freshwater input of both the Amazon and main local rivers. Between 20 and 50 km offshore the combination of riverine nutrient

inputs and decreased turbidity creates a productive zone with high chlorophyll concentrations, termed the green water zone. Offshore from this zone, irradiance further increases, but nutrients become limited for primary production. This is the *blue water zone*, which stretches offshore to the continental slope.

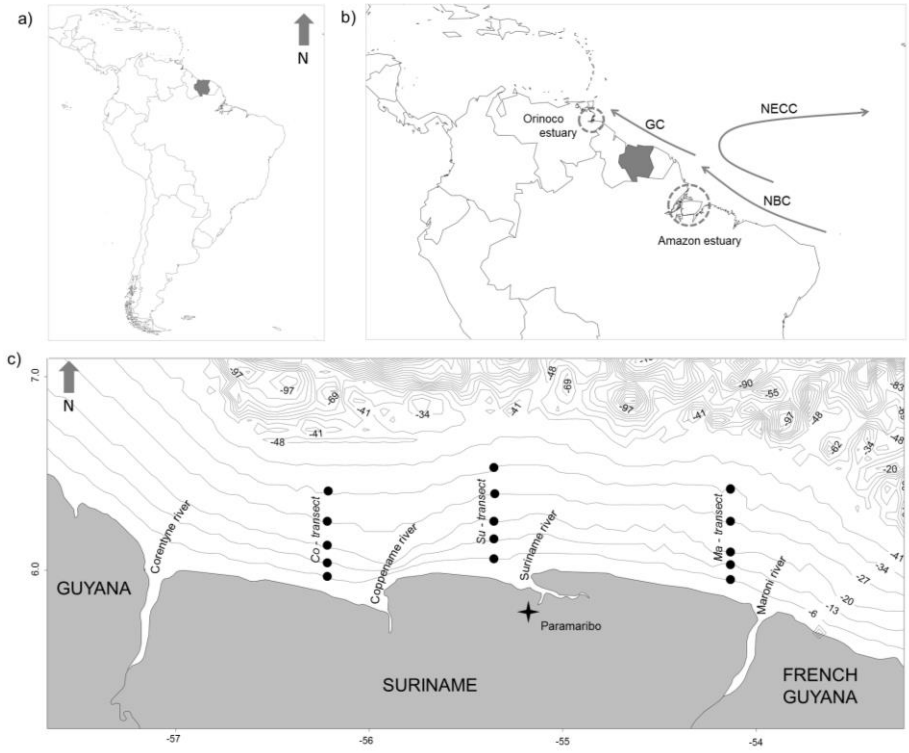


Figure 1. (a) Location of Suriname (shaded in grey). (b) Indication of the Amazon and Orinoco estuary (dashed circles) and the major ocean currents. NBC= North Brazil Current; GC=Guyana Current; NECC=North Equatorial Counter Current. (c) Map of the inner Suriname continental shelf with indication of the major estuaries. Dots represent the sampling sites at 5 depths (6, 13, 20, 27, 34 m) along three transects: Co-transect in the west, Su-transect in the middle, Ma-transect in the east.

2.2 SAMPLING AND DATA ORIGIN

Data originated from 10 trawl surveys for epibenthos and demersal fish conducted between February 2012 and April 2013. Samples were collected at 15 locations situated on 3 transects positioned near the westward directed outflow of the Coppename (Co), Suriname (Su) and Maroni (Ma) rivers (Fig. 1), to detect potential seasonal influences of river outflow on demersal communities. Each transect consisted of 5 locations along a depth gradient (6, 13, 20, 27 and 34 meters depth), starting at the minimum depth for safe vessel operation (6 m) and down to the maximum depth that the vessel's winch

allowed sampling (34 m). Sampling was done onboard Neptune-6, a 25-m long commercial outrigger trawler of the Suriname seabob shrimp (*Xiphopenaeus kroyeri*) trawling fleet (Heiploeg Suriname). A small otter trawl at the stern of the vessel (the 'try-net': 4.3 m horizontal spread; 45 mm stretched cod end mesh size) was used for sampling. This gear type was chosen because it is known to operate well on the often muddy seabed, and it has proven efficient in catching shrimp (so presumably as well other epibenthos).

During each sampling campaign, one trawl sample was collected at each station by towing the trawl for 40 minutes in westward direction at a speed of approximately 2.5 knots. We used normal try-net towing speed and direction, but twice the normal hauling time (20 minutes) to obtain a representative sample. Sampling time, start and stop coordinates and sampling depth were noted to enable a correct conversion towards sampled surface units. All samples were taken during daytime. All stations were sampled monthly for the first 6 months and bi-monthly later on (Table 1). Two samples could not be taken due to drift sein fisheries on the spot (Ma06, January 2013) and technical problems (Ma34, April 2013).

Table 1. Overview of available environmental data for each campaign. STD=salinity/temperature/depth, SECCHI=Secchi-depth, SS-TSM=sub-surface total suspended matter, TOC=sediment total organic carbon, MEDSAND=median grain size of sediment sand fraction, MUD=sediment mud content, CHL=Chlorophyll a, SF-TSM=surface total suspended matter, SST=sea surface temperature.

Nr	Begin	End	Season	Epi	STD	SECCHI	SS-TSM	TOC	MED-SAND	MUD	CHL **	SF-TSM **	SST **
1	17/02/12	22/02/12	rainy	X	X	X	X	X	X	X	X	X	X
2	24/03/12	29/03/12	rainy	X	X	X	X	-	-	-	X	X	X
3	20/04/12	25/04/12	rainy	X	X	X	X	X	X	X	X	X	X
4	22/05/12	29/05/12	rainy	X	X	X	X	X	X	X	X	X	X
5	30/06/12	04/07/12	dry	X	X	X	X	-	-	-	X	X	X
6	21/07/12	26/07/12	dry	X	X	X	X	-	-	-	X	X	X
7	29/09/12	04/10/12	dry	X	-	X	X	-	-	-	X	X	X
8	27/11/12	01/12/12	dry	X	-	X	X	-	-	-	X	X	X
9	29/01/13	03/02/13	dry	X*	-	X	X	-	-	-	X	X	X
10	10/04/13	15/04/13	rainy	X*	-	X	X	-	-	-	X	X	X

* missing data for Ma06 (campaign 9) and Ma34 (campaign 10); ** data originating from remote sensing (MODIS-satellite)

Epibenthos was sorted from the catch and frozen (-20°C) onboard. In the lab, organisms were identified to species or higher taxon level, counted and weighted (wet weight; 0.1 g precision). Species identification was based on, among others, Holthuis (1959), Walenkamp J.H.C. (1976), Takeda and Okutani (1983) and Cervigón et al. (1993). Fish was also retained from the catches, but reported on elsewhere (Willems et al., 2015a).

Several *in-situ* environmental parameters were determined per location (Table 1). Water salinity, temperature and depth were measured with a CTD (SAIV SD200), but data were not recorded for the last four campaigns due to technical problems. Water clarity was measured with a *Secchi*-disk. Sub-surface total suspended matter concentrations (SS-TSM) were measured from water collected at 5 m depth with a Niskin bottle, filtered on pre-washed, pre-weighted GF/F filters and stored at -20°C. Filters were subsequently dried in the lab (48h at 70 °C) and re-weighted (0.0001 g precision) to calculate SS-TSM.

A Van Veen grab was used to collect sediment samples on three campaigns (February, April and May 2012). A sediment subsample was dried in the lab (48h at 70 °C), and analyzed for total organic carbon content (TOC) and grain size composition. For the latter a Malvern Mastersizer 2000G hydro version 5.40 (Malvern, 1999) was used to calculate mud percentage (<63 μm; MUD) and median grain size of the sand fraction (63-2000 μm; MEDSAND).

The above mentioned environmental data were complemented by remote sensing data from the satellite-borne sensor MODIS on the polar-orbiting Aqua satellite (OBPG, 2014; Bailey et al., 2010), including surface total suspended matter concentrations (SF-TSM), chlorophyll *a* concentrations (CHL) and sea surface temperature (SST) (Nechad et al., 2010). MODIS values (spatial resolution of approximately 1 x 1 km) with the best spatial and temporal accordance with *in-situ* sampling were used (see Vanhellemont et al., 2011; Vanhellemont and Ruddick, 2011 for an extensive explanation on the use of this technology).

Rainfall data at 65 land-based stations in Suriname were obtained from the Suriname Meteorological Service. River discharge data for Maroni river (measured at Langa Tabiki, Suriname) and Amazon river (measured at Obidos, Brazil) were available from the Environmental Research Laboratory (ORE-HYBAM, 2014).

2.3 DATA ANALYSES

Sampling campaigns were considered to occur either in the *rainy* or *dry* season based on real-time river outflow data of Maroni River with a cut-off at the mid-range discharge value (2960 $m^3.s^{-1}$). As such, the four campaigns in February to May 2012 were considered as *rainy*. The five following campaigns were *dry* while the last campaign (April 2013) was again *rainy* (Table 1, Fig. 3).

Spatial and temporal variability in environmental variables was tested with a three-way Permanova (Anderson et al., 2008) on an Euclidean distance resemblance matrix with the factors 'depth', 'transect' and 'season'. Sediment parameters were only measured in the *rainy* season and hence only tested for

'depth' and 'transect'. In case of significant effects, pairwise tests were conducted to test for differences within factors. P-values were drawn from Monte Carlo (MC) permutations when the number of possible permutations was restricted (<100) (Anderson and Robinson, 2003). Correlations between rainfall and river discharge were tested with Pearson product moment correlations after the data appeared normally distributed (Shapiro-Wilk normality test; $p>0.05$).

Epibenthos data were standardized and expressed as numbers and biomass per surface unit (1000 m^2). Multivariate analyses were performed on fourth-root transformed epibenthos abundance data using the Bray-Curtis similarity index with exclusion of rare species (occurring in <3 % of the samples; Table 2), to reduce the influence of highly abundant and rare species, respectively.

Distance-based linear models (DistLM) based on BEST selection and BIC criterion were used to relate patterns in species composition and abundance to the nine calculated environmental variables: CHL, SF-TSM, SS-TSM, SST, Maroni discharge, Amazon discharge, *Secchi*-depth, MEDSAND, and TOC. As sediment was only three times sampled, averages per location were calculated from these campaigns and used for the missing months (this approach was validated by a DistLM analysis with only the three campaigns, giving similar results as the full DistLM analysis). Environmental data were normalized and collinearity among variables was examined using Spearman rank correlation coefficients prior to the DistLM analyses. For linear dependent variables ($|r| \geq 0.8$) only one variable was retained in the analysis. As such, depth, rainfall and MUD were excluded from the analyses, due to collinearity with TOC, Maroni discharge and TOC, respectively.

In a next step, cluster analyses with SIMPROF tests (1 % significance level) were performed to investigate the epibenthic community structure, based on Bray-Curtis similarity index for the fourth root transformed species abundance matrix. The significance level was set more stringent given the multiple testing inherent in this hierarchical approach as suggested in Clarke et al. (2008). Following, a SIMPER analysis (cut-off 90 %) was performed to specify the discriminating species within the observed clusters. The clusters were further characterized in terms of density (N), biomass (B), species richness (S), Shannon Wiener diversity (H') and Pielou's evenness (J'), and in terms of the relevant (DistLM-based) environmental variables. Significant differences in these univariate parameters between cluster groups were tested through one-way Permanova analyses, based on the Euclidean distance resemblance matrix with unrestricted permutation of raw data (Anderson et al., 2008) and through pairwise tests. Monte Carlo (MC) corrections were applied when too few (<100) permutations could be calculated (Anderson and Robinson, 2003).

Within-cluster patterns in species composition and abundance were further investigated for small-scale spatial and temporal patterns, using a three-way Permanova design with the factors 'depth', 'transect' and 'season'. These analyses were based on a Bray-Curtis similarity index constructed of fourth-root transformed epibenthos abundance data for all samples per cluster. Finally, within-cluster variation in the univariate parameters was tested using a similar three-way Permanova design based on an Euclidean distance resemblance matrix. All data analyses were performed in R v.3.0.1 (R Core Team, 2013) and in PRIMER v.6.1.13 with Permanova add-on software (Clarke and Gorley, 2006; Anderson et al., 2008). A significance level of p=0.05 was used in all tests. Throughout the text, averages are always given together with their standard deviation (SD).

3 RESULTS

3.1 ENVIRONMENTAL CHARACTERISATION

3.1.1 SPATIAL VARIABILITY

Most water parameters were significantly influenced by the factor 'depth' (Annex 2.1, Fig.2), corresponding with an inshore-offshore gradient. Chlorophyll *a* concentrations (CHL) steadily decreased from the 6m-locations (average 5.2 ± SD 2.1 $mg.m^{-3}$) towards the 34m-locations (1.6 ± 1.4 $mg.m^{-3}$) and differed significantly between most depths (pairwise tests), except between 13 and 20 m (pseudo-F=24.2, p=0.0001). Similarly, sub-surface total suspended matter concentrations (SS-TSM) decreased from 99.0 ± 53.7 $g.m^{-3}$ at 6m-depths to 36.0 ± 11.3 $g.m^{-3}$ at 34m-depths (Pseudo-F=27.9; p=0.0001), and also most pairwise tests for the factor 'depth' were significant. On the contrary, sea surface temperatures (SST) were significantly higher at the 6m-locations (28.7 ± 1.2 °C) compared to the 20, 27 and 34 m locations together (avg. 27.8 ± 1.0 °C) (pseudo-F=3.1; p=0.0188) and separately (pairwise tests).

The parameters *Secchi*-depth and surface total suspended matter concentration (SF-TSM) were significantly influenced by the interaction factor 'depth x transect' (Annex 2.1, Fig.2). Per transect, the 6m-locations had significantly lower *Secchi*-depths compared to the 34m-locations (Pseudo-F=3.5; p=0.001), while in the Su-transect *Secchi*-depth was significantly lower than in the Co-transect (at 6m-depth) and the Ma-transect (at all other depths, pairwise tests). On the contrary, SF-TSM was significantly higher at the 6m-locations compared to the 34m-locations in all transects (Pseudo-F=2.2; p=0.0301), with some local differences between the three transects (pairwise tests). For salinity (avg. 34.9 ± 0.9, measured at 5 m below water surface) no significant spatial differences were noted.

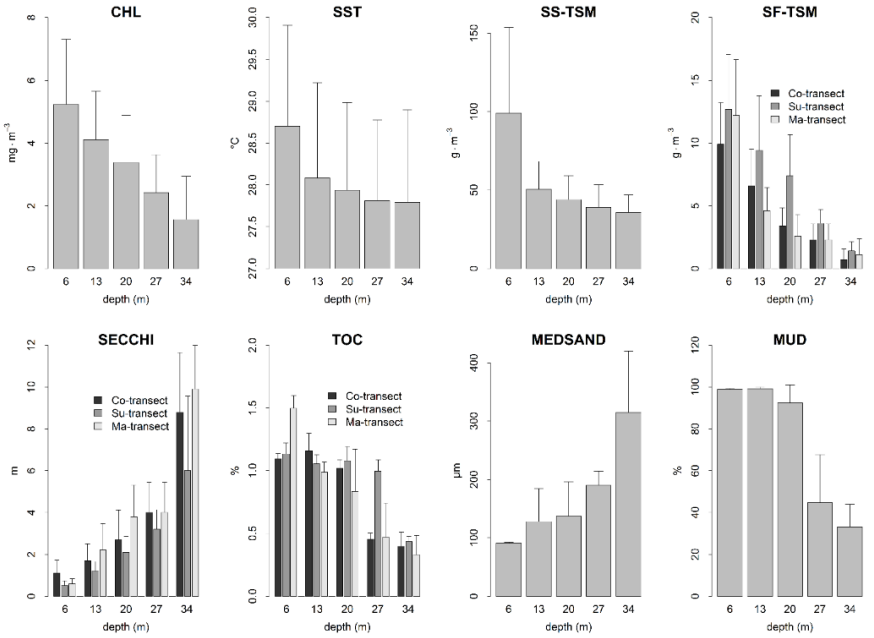


Figure 2. Barplots (average + SD) of water and sediment parameters. CHL=remote sensing chlorophyll *a* values; SST=remote sensing sea surface temperature; SS-TSM=*in situ* measured sub-surface total suspended matter; SF-TSM=remote sensing surface total suspended matter; SECCHI=*in situ* measured *Secchi*-depth; TOC=total organic carbon content; MEDSAND=median grain size of sand fraction; MUD=sediment mud content; (the latter three derived from *in situ* bottom-grab samples).

Also, the three sediment characteristics were significantly influenced by the factor 'depth' and show±ed a clear inshore-offshore gradient (Annex 2.1; Fig.2). The sand fraction (MEDSAND) increased from the 6m-locations (90.8 ± 1.8 µm) towards the 34m-locations (318.1 ± 105.8 µm) (Pseudo-F=6.0; p=0.0056). In the pairwise tests, significant differences in MEDSAND were mainly noted between the 34m-locations and most other locations except the 27m-locations. On the contrary, high MUD values were noted at all 6m-, 13m- and 20m-locations (avg. 96.8 ± 5.9 %), which were significantly different from the lower values at the 27m- and 34m-locations (avg. 38.9 ± 18.7 %) in the pairwise tests.

For total organic carbon content of the sediment (TOC), a significant interaction 'depth x transect' was detected as well (Pseudo-F=4.4; p=0.0072) (Annex 2.1, Fig.2). In the Ma-transect, a steady decrease with depth was observed from 1.5 % at 6m-depth to 0.3 % at 34m-depth, with the main pairwise differences noted between the 6m-location and the other depths. In both the Su- and Co-transect, a sudden significant drop in TOC was observed near the 34m and 27m-locations, respectively, compared to the shallower locations (pairwise tests).

3.1.2 SEASONAL VARIABILITY

In 2012, most land rainfall was noted between January and August (on average 221 ± 53 mm per month). The period September 2012 - January 2013 was much drier with an average rainfall of 60 ± 28 mm, after which the rainfall increased again (Fig. 3).

The average monthly Maroni river discharge largely followed this rainfall pattern with a peak-discharge over 5000 $m^3.s^{-1}$ in April 2012 and a minimum flow of 126 $m^3.s^{-1}$ in November 2012. The correlation was stronger when taking into account a one-month time lag between rainfall and Maroni discharge (Pearson r=0.73; p=0.002). Also, a similar discharge pattern was noted for the Amazon River (Pearson r=0.81; p=0.0001), with a peak flow in July 2012 and a minimum flow in November 2012. The peak volume discharged by the Amazon River was about 260.000 $m^3.s^{-1}$, nearly 50 times the Maroni peak-discharge volume (Fig. 3).

CHL, SS-TSM and SST were significantly influenced by the factor 'season' but not by any interaction term (Annex 2.1). In the *rainy* season, all locations were characterized by significantly higher CHL (3.7 ± 2.2 $mg.m^{-3}$ *vs.* 3.0 ± 1.7 $mg.m^{-3}$ in the *dry* season) (Pseudo-F=7.9; p=0.0056). Also, SS-TSM was higher in the *rainy* season (60.6 ± 36.7 $g.m^{-3}$ *vs.* 46.5 ± 32.9 $g.m^{-3}$) (Pseudo-F=8.6; p=0.0035). On the other hand, SST was significantly higher in the *dry* season (28.3 ± 1.2 °C) than in the *rainy* season (27.9 ± 1.0 °C; Pseudo-F=4.1; p=0.0443). Elevated SST-values preceded low river discharge (Pearson r=-0.80; p=0.0003 for SST and one month time-lag Maroni discharge).

For the parameters SF-TSM, *Secchi*-depth and salinity no significant 'seasonal' effect was observed. Sediment parameters where only measured in the *rainy* season and could not be tested for 'seasonal' interactions.

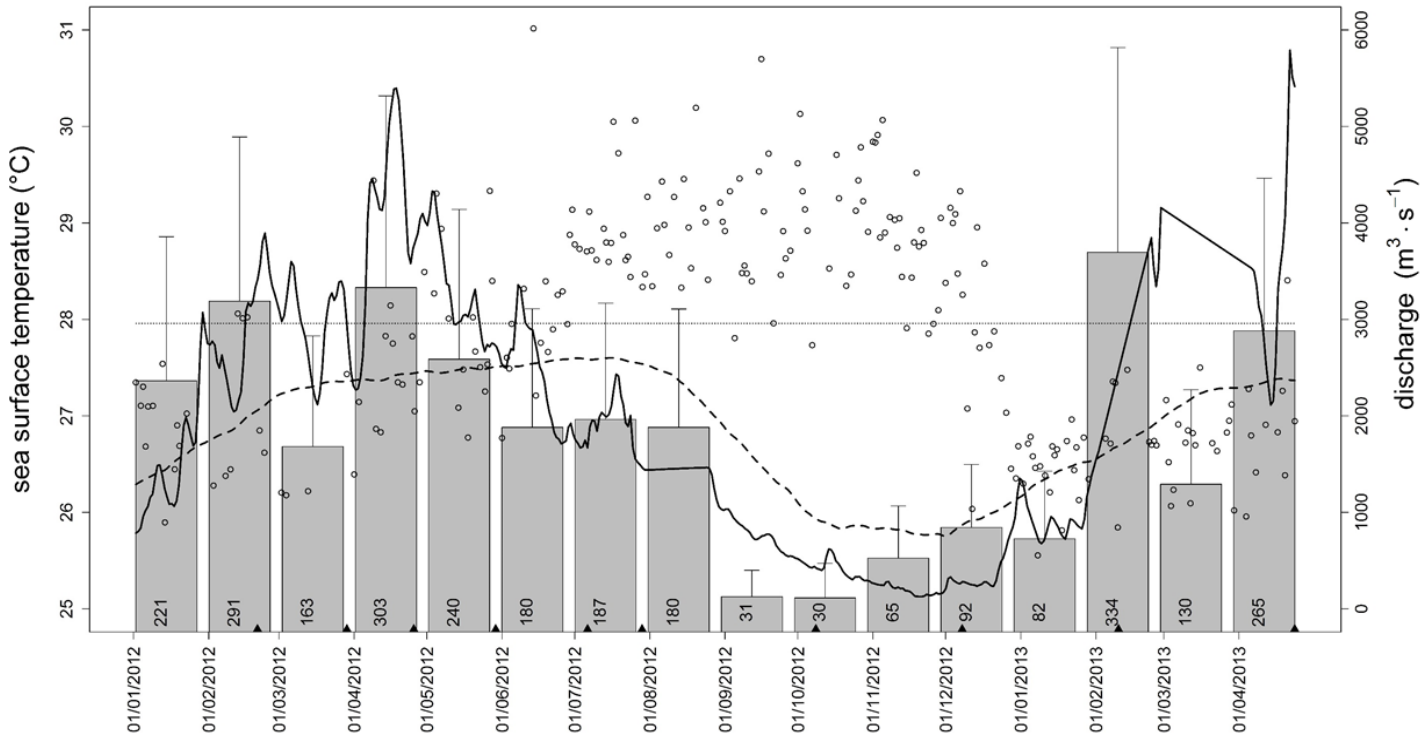


Figure 3. Rainfall, sea surface temperature and river discharge over time during the study. Bars: average (+SD) monthly rainfall at 62 land-based stations in Suriname; vertical numbers at bar-base denote average rainfall in mm; black triangles indicate sampling campaigns. Open dots: *remote sensing* sea surface temperature, averaged over 15 sampling locations (left axis). Solid line: daily discharge of Maroni River measured at Langa Tabiki (right axis); the horizontal dashed line indicates the cut-off Maroni discharge value between *dry* and *rainy season*. Dashed line: daily discharge of Amazon river measured at Obidos (Brazil) (right axis); discharge values for Amazon have been divided by 100 for visualization purposes.

3.2 EPIBENTHOS CHARACTERISATION

3.2.1 GENERAL

From the 148 bottom-trawl samples, 92 epbenthic taxa, further referred to as species, were identified. Crustaceans were the most abundant group with 41 species, followed by molluscs (31 species) and echinoderms (14 species). Three cnidarians, a polychaete, a tunicate and a sponge (Porifera) completed the list (Table 2). Samples contained between 1 and 31 epibenthic species with on average 6.6 ± 4.7 species per sample. Density ranged from 0.2 to 1392 ind.1000 m^{-2}, wet weight biomass from 0.8 to 6675 g.1000 m^{-2}. Overall, Atlantic seabob shrimp *Xiphopenaeus kroyeri* was the dominant species, accounting for 61 ± 43 % of the total density and occurring in 70 % of all samples. Carapace length of *X. kroyeri* ranged from 9 to 33 mm and was on average 20.7 ± SD 3.9 mm. Other abundant species (occurring in 50 to 60 % of the samples) were brown shrimp *Penaeus subitis* (9 ± 20 %), soft coral *Renilla muelleri* (7 ± 17 %), brittle star *Ophioderma brevispina* (7 ± 19 %) and blue swimming crab *Callinectes ornatus* (2 ± 6 %). Many species were rare: 25 species only occurred in one sample, while 64 species were found in <5 % of the samples.

Demersal fishes were abundant in the trawl catches, with *Stellifer rastifer, Amphiarius rugispinis* and *Cynoscion jamaicensis* being the most dominant species by number. A description of the demersal fish community based on this survey can be found in Willems et al.(2015a).

3.2.2 DELINEATION OF EPIBENTHIC ASSEMBLAGES

After omitting rare species (occurring in < 3 % of the samples), 44 of the 92 epibenthic species were retained for further analyses. Hierarchical clustering of the samples discriminated 6 outliers and three main cluster groups at the 28 % similarity level (Fig. 4). The largest cluster contained nearly all samples located at the 6, 13 and 20m-depths, supplemented with most of the 27m-samples of the Ma-transect. This cluster is further referred to as the *coastal assemblage*. A second large cluster is called the *transition assemblage*, containing the remaining samples at 27m-depth of the Co- and Su-transects and the 34m-depth samples of Ma-transect. The third cluster (i.e. the *offshore assemblage*) contained the 34m-samples of the Co- and Su-transects (Fig.4 and Fig. 5).

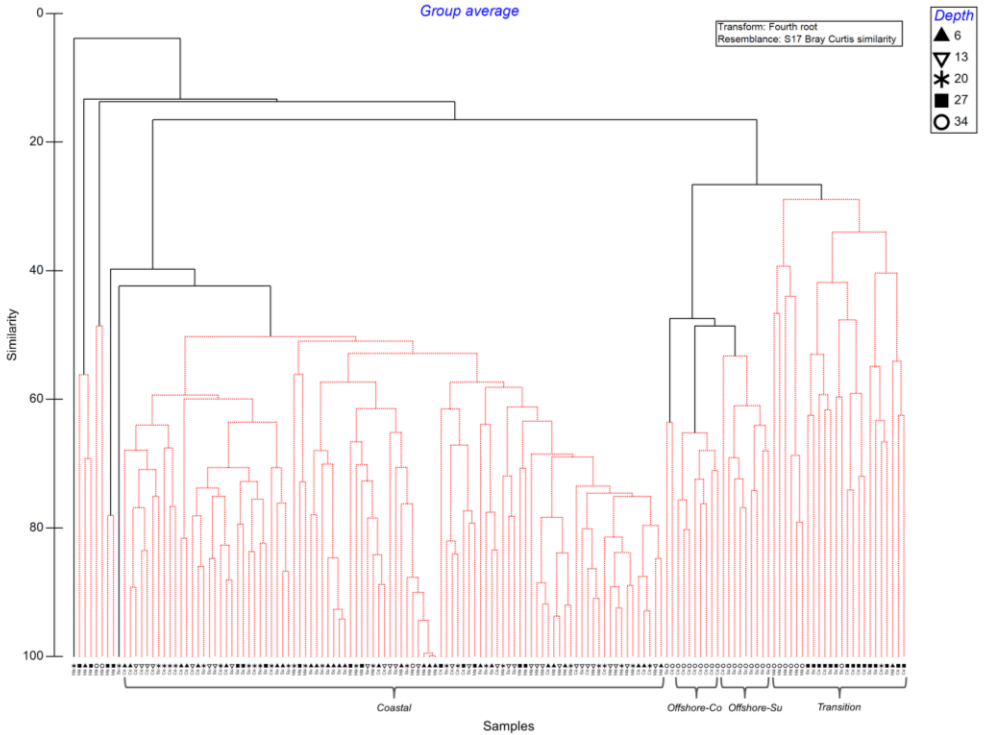


Figure 4. Group-average cluster analysis based on Bray-Curtis resemblance matrix of fourth-root-transformed species abundance data in all epibenthos samples. Significant clusters (SIMPROF test, 1 % significance level) are indicated by the coloured (red) lines. Samples are labeled with depth (symbol) and transect (Co=Coppename; Su=Suriname; Ma=Marowijne transect). Assemblages are identified at the 28 % similarity level (dashed line).

Table 2. List of epibenthic taxa identified from the trawl samples.

CRUSTACEA

Decapoda - Penaeoidea

Penaeus brasiliensis Latreille, 1817

Penaeus notialis Pérez Farfante, 1967 *

Penaeus subtilis Pérez Farfante, 1967

Penaeus schmitti Burkenroad, 1936

Sicyonia typica Boeck, 1864 *

Sycionia sp. H. Milne Edwards, 1830 *

Xiphopenaeus kroyeri Heller, 1862

Decapoda - Anomura

Clibanarius foresti Holthuis, 1959

Dardanus fucosus Biffar & Provenzano, 1972

Ostraconotus spatulipes A. Milne-Edwards, 1880 * §

Paguroidea sp. 1 Latreille, 1802 *

Paguroidea sp. 2 Latreille, 1802 *

Petrochirus diogenes Linnaeus, 1758

Porcellana sayana Leach, 1820

Decapoda - Brachyura

Acanthilia intermedia Miers, 1886 *

Achelous spinimanus Latreille, 1819 *

Brachyura sp. 1 Linnaeus, 1758 *

Brachyura sp. 2 Linnaeus, 1758 *

Calappa nitida Holthuis, 1958

Calappa sulcata Rathbun, 1898

Callinectes bocourti A. Milne-Edwards, 1879

Callinectes danae Smith, 1869 *

Callinectes ornatus Ordway, 1863

Collodes inermis A. Milne-Edwards, 1878 *

Hepatus gronovii Holthuis, 1959

Hepatus pudibundus Herbst, 1785 *

Stomatopoda

Squilla empusa Say, 1818

Squilla lijdingi Holthuis, 1959

Squilla rugosa Bigelow, 1893 *

ECHINODERMATA

Asteroidea

Astropecten americanus Verrill, 1880 *

Astropecten brasiliensis Müller & Troschel, 1842

Astropecten marginatus Gray, 1840

Echinaster guyanensis A.M. Clark, 1987

Luidia alternata Say, 1825

Luidia clathrata Say, 1825

Luidia senegalensis Lamarck, 1816

Ophiuroidea

Astrophyton muricatum Lamarck, 1816 §

Ophioderma brevispina Say, 1825 §

Ophiolepis elegans Lütken, 1859 §

Crinoidea

Tropiometra carinata Lamarck, 1816 * §

Echinoidea

Eucidaris tribuloides Lamarck, 1816 * §

Hygrosoma petersii A. Agassiz, 1880 * §

Holothuroidea

Holothuroidea sp. *

MOLLUSCA

Bivalvia

Adrana gloriosa A. Adams, 1856 *

Aequipecten lineolaris Lamarck, 1819 *

Cephalopoda

Cephalopoda sp. Cuvier, 1795

Doryteuthis pleii Blainville, 1823 *

Doryteuthis surinamensis Voss, 1974

Octopodidae sp. 1 d'Orbigny, 1839 *

Octopodidae sp. 2 d'Orbigny, 1839 *

Gastropoda

Conus compressus G.B. Sowerby II, 1866 *

Distorsio clathrata Lamarck, 1816

Fusinus ansatus Gmelin, 1791 *

Gastropoda sp. 1 Cuvier, 1795 *

Gastropoda sp. 2 Cuvier, 1795 *

Marsupina bufo Bruguière, 1792

Murex sp. 1 Linnaeus, 1758 *

Murex sp. 2 Linnaeus, 1758 *

Phyllonotus pomum Gmelin, 1791 *

Pugilina morio Linnaeus, 1758 §

Terebra taurina Lightfoot, 1786 *

Tonna galea Linnaeus, 1758

Turritella variegata Linnaeus, 1758 * §

CNIDARIA

Anthozoa

Anthozoa sp. Ehrenberg, 1834

Renilla muelleri Kölliker, 1872 §

Virgularia sp. Lamarck, 1816 *

PORIFERA

Porifera sp. Grant, 1836 *

Table 2. continued.

Hepatus scaber Holthuis, 1959 *
Hypoconcha arcuata Stimpson, 1858 *
Iliacantha liodactylus Rathbun, 1898 *
Lupella forceps Fabricius, 1793
Moreiradromia antillensis Stimpson, 1858 *
Paradasygyius tuberculatus de Castro, 1949
Persephona lichtensteinii Leach, 1817
Podochela riisei Stimpson, 1860
Portunus gibbesii Stimpson, 1859
Stenorhynchus seticornis Herbst, 1788

Decapoda - Caridea

Exhippolysmata oplophoroides Holthuis, 1948
Nematopalaemon schmitti Holthuis, 1950

Amygdalum politum Verrill & Smith, 1880 *
Anadara notabilis Röding, 1798
Arcinella arcinella Linnaeus, 1767 *
Argopecten gibbus Linnaeus, 1758 §
Argopecten nucleus Born, 1778 §
Bivalvia sp. 1 Linnaeus, 1758 *
Dallocardia muricata Linnaeus, 1758 * §
Euvola chazaliei Dautzenberg, 1900 *
Modiolus squamosus Beauperthuy, 1967 §
Pinnidae sp. 1 Leach, 1819 *
Trachycardium isocardia Linnaeus, 1758 *

ANNELIDA

Polychaeta sp. 1 Grube, 1850 *

TUNICATA

Ascidiacea

Ascidiacea sp. Nielsen, 1995 *

* = rare species (occurring in < 3 % of the samples)

§ = no previous record for Suriname was found

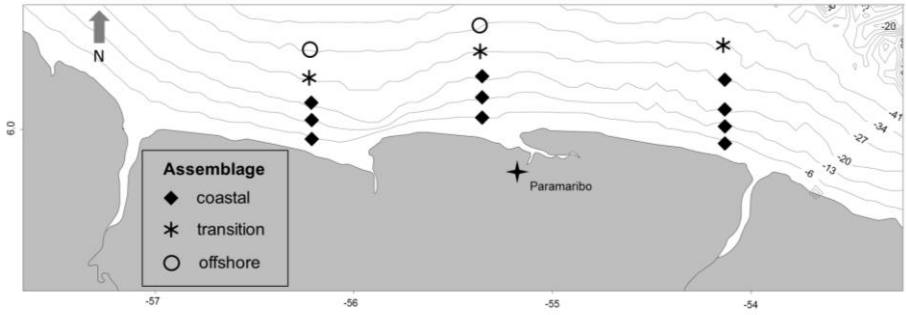


Figure 5. Map of the study area with the three epibenthic asseblages plotted at the 15 locations, sampled along 5 parallel depths (6, 13, 20, 27, 34m) and 3 longitudinal transects (Co-transect in the west, Su-transect in the middle, Ma-transect in the east).

3.2.3 SPATIO-TEMPORAL PATTERNS IN THE EPIBENTHIC ASSEMBLAGES

Overall, no temporal differences in epibenthic species composition and abundance were observed in either the *coastal* or the *transition assemblage*. Only within the *coastal assemblage* a significant effect for the factor 'season' was noted for Pielou's eveness index J' (Pseudo-F=5.0; p=0.03), being higher in the *rainy* season. Secondly, a significant 'transect x season'-interaction was found for Shannon diversity index H' (Pseudo-F=3.8; p=0.03), which was higher in the *rainy* season in the Co-transect (Annex 2.2b). In the *offshore assemblage*, species composition and abundance differed between the *dry* and *rainy* season (Pseudo-F=2.1; p=0.03), but no differences in diversity indices were observed.

As shown above, mainly spatial differences were noted in the epibenthic community. The linear combination of environmental variables that best explained the variation in the multivariate data cloud included TOC (21 %), MEDSAND (20 %) and *Secchi*-depth (16 %). When fitted together (DistLM BEST - BIC; p=0.0001), these variables explained 27 % of the total variation in the epibenthic community structure (Fig. 6).

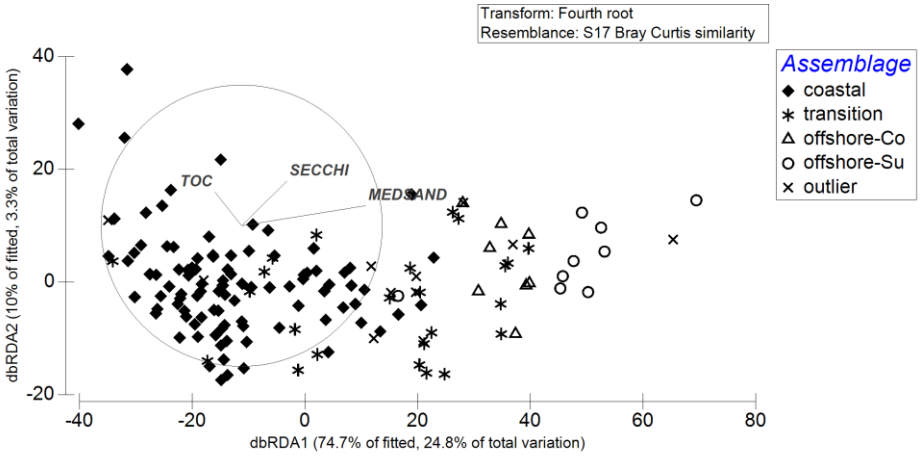


Figure 6. Distance-based redundancy analysis (dbRDA) plot of all epibenthic samples (fourth-root transformed density values; Bray-Curtis similarity) and 9 environmental predictor variables. Symbols represent species assemblages delineated from hierarchical clustering (28 % similarity level). The three variables selected to fit the best model in DistLM are overlaid as vectors using multiple correlation. TOC = sediment total organic carbon; SECCHI = *Secchi*-depth; MEDSAND = median grain size of the sand faction.

Significant differences were observed between the three assemblages for total epibenthic density (Pseudo-F=5.5; p=0.0087), biomass (Pseudo-F=5.6; p=0.0089), species richness (Pseudo-F=89.1; p=0.0001), Shannon diversity (Pseudo-F=149.9; p=0.0001) and Pielou's evenness (Pseudo-F=43.6; p=0.0001). Pairwise comparisons revealed that epibenthic density and biomass in the *coastal assemblage* attained significantly higher values (on average 2 to

3 times higher) than the *transition* and *offshore assemblages* (Fig. 7, Table 3). Species richness differed significantly among all assemblages (pairwise tests; p<0.01) and gradually increased from the *coastal assemblage* (4.8 ± 2.6) to the *offshore* assemblages (14.6 ± 4.1). Also, Pielou's evenness and Shannon diversity indices were significantly lower in the *coastal assemblage*.

Similarly, significant differences were observed between the three assemblages for the three environmental parameters that explained most of the variance in the data, namely TOC (Pseudo-F=57.9; p=0.0001), MEDSAND (Pseudo-F=106.0; p=0.0001) and *Secchi*-depth (Pseudo-F=40.9; p=0.0001). Pairwise comparisons further revealed that the *coastal assemblage* had significantly higher TOC, lower MEDSAND and lower *Secchi*-depth compared to the other two assemblages (Fig. 7, Table 3).

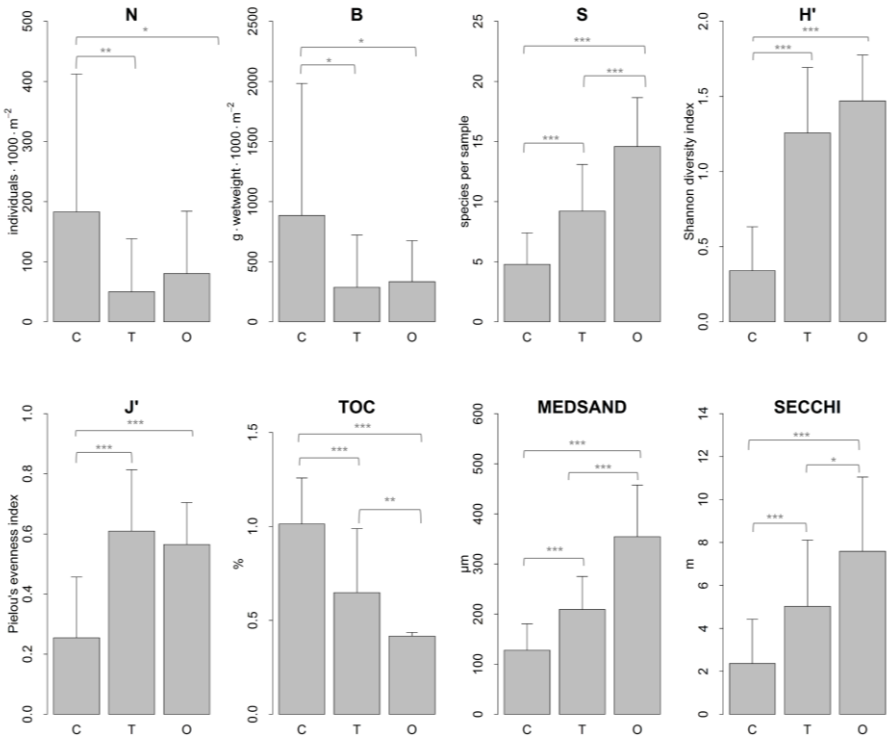


Figure 7. Barplots showing main characteristics of the three assemblages (C=*coastal*, T=*transition*, O=*offshore assemblages*) as defined by cluster analysis (averages + SD). N=density, B=biomass, S=species richness, H'=Shannon-diversity, J'=Pielou's evenness, TOC=sediment total organic carbon, MEDSAND=median grain size of sand faction, SECCHI=*Secchi*-depth. Significant differences between communities as defined by Permanova are indicated (*p=0.01-0.05, **p=0.001-0.01, ***p<0.001).

One-way SIMPER analyses revealed that the *coastal assemblage* was dominated by seabob shrimp *Xiphopenaeus kroyeri*, contributing 74% to within-group similarity (Table 3, Fig. 8). Other characterizing species were brown shrimp *Penaeus subtilis*, soft coral *Renilla muelleri* and blue swimming crab *Callinectes ornatus*. The latter three species together with hermit crab *Clibanarius foresti* were the most important species contributing to within-group similarity in the *transition assemblage*. The *offshore assemblage* was characterized by brittle stars *Ophioderma brevispina* and *Ophiolepis elegans*, and starfish *Luidia clathrata* and *Luidia senegalensis* as important contributors to within-group similarity.

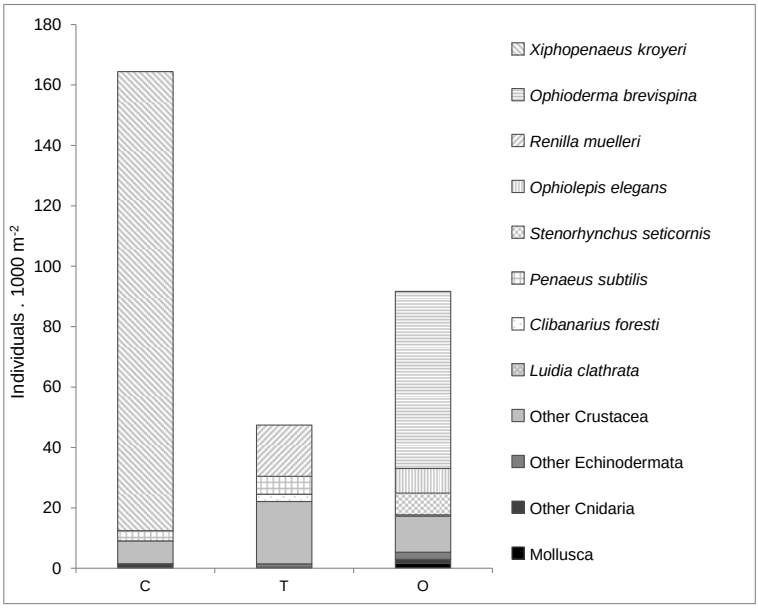


Figure 8. Average epibenthic density per assemblage with indication of the most important species (>10% SIMPER contribution). Average densities for all other species are given per taxonomic group. C=*coastal*, T=*transition*, O=*offshore assemblage*.

Table 3. Characterization of the three species assemblages defined by cluster analysis, showing average 'within group' similarity based on one-way SIMPER analysis of fourth-root transformed abundance data. Species accounting for 90% cumulative contributing of the 'within group' similarity are listed along with their contribution (Contrib%). Also the average (± SD) per assemblage for a number of univariate parameters is given. TOC: sediment total organic carbon, MEDSAND: median grain size of the sand faction, SECCHI: *Secchi*-depth.

	Coastal community (avg. sim. = 54.4%)		Transition community (avg. sim. = 36.6%)		Offshore community (avg. sim. = 54.4%)	
	Species	Contrib%	Species	Contrib%	Species	Contrib%
	Xiphopenaeus kroyeri	73.5	*Penaeus subtilis*	21.3	*Ophioderma brevispina*	21.5
	Penaeus subtilis	9.9	*Renilla muelleri*	18.8	*Ophiolepis elegans*	13.6
	Renilla muelleri	5	*Clibanarius foresti*	11.3	*Luidia clathrata*	9.5
	Callinectes ornatus	4.9	*Callinectes ornatus*	8.5	*Luidia senegalensis*	8.1
			Luidia senegalensis	8.4	*Dardanus fucosus*	6.6
			Dardanus fucosus	5.9	*Portunus gibbesii*	5.6
			Doryteuthis surinamensis	4.5	*Argopecten gibbus*	5
			Paradasygyius tuberculatus	4.5	*Clibanarius foresti*	4.7
			Porcellana sayana	3.8	*Stenorhynchus seticornis*	4
			Anthozoa sp.	2.1	*Renilla muelleri*	3.2
			Marsupina bufo	2.1	*Callinectes ornatus*	3.1
					Doryteuthis surinamensis	2.5
					Astropecten brasiliensis	2.2
					Echinaster guyanensis	2.2
N samples	99		24		19	
Density (ind.1000 m^{-2})	183 ± 229		50 ± 88		80 ± 104	
WW Biomass (g.1000 m^{-2})	885 ± 1098		293.1 ± 432.4		335 ± 341	
Species richness S	4.8 ± 2.6		9.2 ± 3.9		14.6 ± 4.1	
Shannon Diversity H	0.3 ± 0.3		1.3 ± 0.4		1.5 ± 0.3	
Pielou's Eveness J'	0.3 ± 0.2		0.6 ± 0.2		0.6 ± 0.1	
TOC (%)	1 ± 0.3		0.7 ± 0.3		0.4 ± 0.02	
MEDSAND (μm)	128 ± 53		209 ± 66		345 ± 103	
SECCHI (m)	2.4 ± 2.1		5 ± 3.1		7.6 ± 3.5	

Although three epibenthic assemblages were discerned, each assemblage grouped several significant sample clusters based on SIMPROF tests (Fig.4). This variation was reflected in some spatial differences in species composition and abundance within each assemblage (Annex 2.2a). A significant 'depth x transect' interaction occurred in the *coastal assemblage* (Pseudo-F=1.8; p=0.006). Pairwise tests revealed significant differences between depths in each transect, and between transects at each depth (pairwise tests, p<0.05). SIMPER results indicated a decreasing dominance of *X. kroyeri* with depth and

from east (Ma-transect) to west (Co-transect) in the *coastal assemblage*. Within the transition assemblage a significant effect of the factor 'transect' was found (Pseudo-F=3.3; p=0.0002) with the Ma-transect being significantly different from the Su- and Co-transects (pairwise tests, p<0.01). In the *transition assemblage*, the number of species contributing to within-group similarity increased from east to west. Within the *offshore assemblage*, species composition and abundance differed significantly between the Co-transect and the Su-transect (Pseudo-F=7.9; p=0.0002), with epibenthic biomass being significantly higher in the Co-transect than in the Su-transect (Pseudo-F=5.8; p=0.0222). SIMPER results also revealed a slightly different species composition in both offshore locations. For example, arrow crab *Stenorhynchus seticornis* was abundant in the offshore Co-location, while this species was nearly absent from the Su-transect.

Furthermore, within-cluster differences in S, H' and J' occurred. Within the *coastal assemblage*, S increased significantly from 6m to 27m-depth locations (Pseudo-F=8.4; p=0.0005, significant differences, except between 20 and 27m). On the other hand, a significant decrease in S was noted from the Co-transect to the Ma-transect (Pseudo-F=12.0; p=0.0001). A similar patters was seen for H' ('depth x transect'-interaction; Pseudo-F=2.4; p=0.0425). Within the *transition assemblage*, a significant effect of 'transect' was found for S and J' (resp. Pseudo-F=5.0; p=0.0208 and Pseudo-F=11.2; p=0.0008), with the Ma-transect having significantly lower S and higher J' compared to the Co- and Su-transects.

4 DISCUSSION

The current study describes the epibenthic community structure in the coastal waters of Suriname. In total, 92 epibenthic species were identified from the trawl samples, mainly crustaceans and molluscs. Although the mesh size of our trawl gear was rather large for an epibenthic survey, we did capture the species to be expected within the area (e.g. Holthuis, 1959; Takeda and Okutani, 1983) and found 14 species with no previous reference for Suriname. Epibenthic organisms play an important role in tropical soft-bottom ecosystems (e.g. Robertson et al., 1992), and are the only benthic invertebrates in areas where the seabed is too unstable to support infauna (Aller and Aller, 1986). Although the epibenthic species of the Suriname Shelf are generally known, they have never been quantified or described in their ecological context. Knowledge on the spatio-temporal distribution in relation with the environment is crucial to understand the functioning of the coastal ecosystem, and forms the ecological basis for a sustainable management (Reiss et al., 2010).

4.1 SPATIAL PATTERNS

The epibenthic community in the Suriname coastal system was largely structured by spatial differences in the environment. Both sediment and water parameters showed a clear inshore to offshore gradient. Up to the 20m-depth contour, muddy deposits dominated, while further offshore, at higher depths, sediment grain size became coarser. Mud predominantly originates from the Amazon River, which provides an enormous flux of suspended matter into the ocean each year (Salisbury et al., 2011). From the river mouth, mud migrates both in suspension and in the form of mudbanks along the coast in a northwest direction, creating a dynamic 'mud belt' in the intertidal and shallow subtidal zone of the Guianas (Anthony et al., 2010). In Suriname this 'mud belt' is restricted to the area below the 20m-isobath, beyond which it gradually mixes with coarser sediments of the outer shelf (Augustinus, 2004; Eisma et al., 1991).

The term community usually indicates a group of species occurring in a particular place or physical habitat (Mills, 1969). Based on the definitions to delineate biological communities given by Morin (1999), a single epibenthic coastal species assemblage could be discerned in the muddy coastal environment, overall dominated by Atlantic seabob shrimp *Xiphopenaeus kroyeri*, an r-selected, fast growing and mobile species (Branco et al., 1994). This Penaeid shrimp is known to prefer fine substrates (Freire et al., 2011) and to complete its life cycle in estuarine and coastal environments (e.g. Dall et al., 1990). Furthermore, the *coastal assemblage* was species-poor with on average <5 species per sample. Environmental stress in the coastal environment is naturally high (Elliott and Quintino, 2007): deposition and resuspension of fine sediments by tides and currents cause turbid waters and unstable seabeds, and salinity highly varies due to extensive river runoff (Nittrouer and Demaster, 1996). Only few epibenthic and other species can cope with such conditions. In general, tropical shelves under severe river-influences show reduced epifaunal and infaunal populations (Aller and Aller, 2004).

Although the infauna of the Suriname Shelf has been poorly studied, a few studies confirm low densities of macrobenthic animals in the nearshore muddy sediments. Whereas densities of Tanaidacea (Arthropoda: Crustacea) up to 6000 ind. m^{-2} were observed on the higher intertidal mudbanks, total infauna density decreased to 245 ind. m^{-2} in the lower, more unstable mudbanks (Swennen et al., 1982). In the shallow subtidal area (up to ca. 20 m depth) macrobenthic densities were even lower (around 40 ind. m^{-2}), with the dominant taxa being Magelonidae (Annelida: Polychaeta), Marginellidae (Molluca: Gastropoda) and Tanaidacea (ESC, 2011). Rather than by macro- or meio-infauna, benthic communities on tropical river-influenced shelves are dominated by bacteria, accounting for >95 % of the total benthic biomass (Aller and Stupakoff, 1996; Aller et al., 2010). Moreover, Aller & Blair (2006) showed that bacteria efficiently mineralize organic carbon within the Amazon-borne mud, resulting in low sediment total organic carbon values. As such, the high

bacterial biomass may explain the low total organic carbon values of 1% we observed, which is remarkably low for an area with high sediment deposition rates (e.g. Aller, 1998).

High concentrations of *X. kroyeri* are known to occur around 20 m depth, as the major seabob shrimp fishing grounds are located in this zone (Bhagwandin, 2012), known as the *green water zone* (Lowe-McConnell, 1962). In Guyana (Cadée G.C., 1975) and within the Amazon plume (Smith and Demaster, 1996), this zone coincided with a midshore peak in primary production, stimulated by increased irradiance due to flocculation of suspended matter from the surface layer. We also observed a shift from brown to greenish waters around the 20 m isobath on several sampling campaigns. Also, surface total suspended matter was lower than sub-surface suspended matter in this area, but no peak in primary production was measured. Most probably, chlorophyll a measurements were biased due to the high water turbidity (Dall'Olmo et al., 2005). Several authors already noted that real patterns in primary production in near-shore coastal areas may be masked when based on MODIS measurements (e.g. Santer and Schmechtig, 2000; Vantrepotte et al., 2013).

Epibenthic biodiversity (S and H') gradually increased with depth. With depth and increasing distance from riverine input, environmental conditions became more stable and more beneficial for other benthic organisms, resulting in a completely different epibenthic species assemblage along the 34 m depth contour. While the *coastal assemblage* was dominated by the long-shore 'mud belt', more local environmental conditions prevailed in the *offshore assemblage*. The latter zone is characterized by lower organic carbon content in the sediment, coarser sediments and clear overlying waters with less chlorophyll a and less suspended matter. These conditions had a positive influence on the epibenthic biodiversity and abundance. With on average 15 epibenthic species per sample, the *offshore assemblage* was three times more diverse than the *coastal assemblage*. Also at higher latitudes (e.g. the North Sea) epibenthic diversity seems higher in deeper and more offshore areas (Callaway et al., 2002a). van Hoey et al. (2004) showed that as a consequence of the unimodal distribution of species along environmental gradients, biological and physical boundaries of benthic communities are not strict and gradual shifts between communities exist. As such, the *transition assemblage* can be seen as a 'hybrid' assemblage, representing the shift between the *coastal* and the *offshore* epibenthic communities. This *transition assemblage* contained a mix of species of secondary importance in both other assemblages, but was mainly characterized by the absence of seabob shrimp *X. kroyeri*.

In addition to a clear on-offshore gradient, also some differences could be observed when proceeding from west to east, both in environmental parameters and the epibenthic communities. In the *coastal assemblage*, species diversity increased from east to west, while the *offshore assemblage* in the west (Co-transect) was characterized by higher average epibenthic densities and

biomasses compared to the Su-transect. Moreover, we could discern three clear epibenthic assemblages along both Co- and Su-transects, while in the east (Ma-transect) the *transition assemblage* was located deeper and no offshore assemblage could be delineated. This seems to be related to the bathymetry and geomorphology of the coastal shelf in Suriname. The zones in the east are wider compared to the more squeezed coastal shelf in the west, meaning that the *offshore assemblage* in the east will probably be located more offshore between the 40 and 50 m isobaths.

4.2 TEMPORAL VARIABILITY

As expected, peak outflow of the domestic rivers in Suriname coincided with peak Amazon discharge, at times of maximum supply of Amazon water to the coasts of the Guianas through the Guiana Current (Hellweger and Gordon, 2002). Elevated sub-surface total suspended matter and chlorophyll a indicated a clear river-influence during the *rainy* season (Smith and Demaster, 1996). However, seasonal fluctuations in the coastal environment did not affect species composition and abundance in the *coastal* or *transition* assemblages. In shallow waters under direct influence of river-runoff the water column is assumed to be fully mixed and to transfer warm and low saline surface water to the bottom (e.g. Pacanowski and Philander, 1981). Moreover, population dynamics of penaeid shrimps, like the dominant seabob shrimp *X. kroyeri*, are known to be related to seasonality in freshwater input (e.g. Galindo-Bect et al., 2000). Therefore, at least for the *coastal assemblage* we expected some seasonal influence on the epibenthos. Most probably the benthos is more likely to respond to changes in bottom-water properties (Pires, 1992), while only (sub-)surface water parameters were available. On the other hand, Longhurst and Pauly (1987) suggested that interannual changes in species composition and relative abundance are more important than seasonal changes within tropical coastal marine ecosystems.

4.3 IMPLICATIONS FOR MANAGEMENT

The fact that benthic communities respond to their environment is well known (e.g.Gray, 2002), and the present study largely confirms the results from epibenthic studies in neighboring French-Guyana (Durand, 1959; Le Loeuff and Cosel, 2000; Guéguen, 2000b). Still, detailed *in-situ* information on benthic communities is needed as a sound basis for local marine management.

Commercial shrimp fisheries in Suriname shifted to shallower waters targeting *X. kroyeri* after the decline of more valuable deep-water species (*Penaeus spp.*). Also in other countries, *X. kroyeri* has become increasingly important as a fisheries resource in recent decades (FAO, 2014a). The present study showed that the epibenthic community in the coastal waters of Suriname was structured by an environmental inshore to offshore gradient, and that *X. kroyeri*

was highly abundant in muddy substrates, which harbor a species-poor epibenthic community without habitat-structuring species. In this environment, the physical impact of commercial shrimp outrigger trawls is expected to be low. Nevertheless, removing large quantities of *X. kroyeri* can impact the ecosystem by affecting an important link in the coastal food web (e.g. Abarca-Arenas et al., 2007). *Xiphopenaeus kroyeri* feeds at a low trophic level, on benthic detritus, microalgae and crustaceans (Cortés and Criales, 1990; Branco, 2005; Kerkhove, 2014), while the species itself constitutes staple food for demersal fishes (Camargo and Isaac, 2004;Quilez, 2014). As such, populations of *X. kroyeri* are probably crucial for energy transfer within the coastal food web, as has been shown for other penaeid shrimp (Abarca-Arenas et al., 2007). Moreover, *X. kroyeri* was found to strongly contribute to the existence and maintenance of benthic communities in southeastern Brazil (Pires, 1992). Whereas this stabilizing role was seasonally taken over by the swimming crab *Portunus spinicarpus* in response to variation in water masses (Pires, 1992), it might be played year-round by *X. kroyeri* on the Suriname Shelf.

Because the benthic communities on the inner Suriname Shelf were mainly spatially structured, with little temporal variation, spatial management measures are likely to be more effective than temporal restrictions. The current ban on all demersal trawl fisheries below 18 m depth indeed seems a valid management measure to ensure the integrity of the coastal food web and to protect demersal fish recruits (Willems et al., 2015a). Still, indirect (trophic) effects of intensive *X. kroyeri* fisheries beyond 18 m depth might occur. Furthermore, the current study only considered adult *X. kroyeri*, while temporal patterns are likely to be important within the younger life stages (Torrez, 2015). Information on the life cycle and ecological role of *X. kroyeri* within the coastal food web of the Suriname Shelf is therefore needed to support an ecosystem-based fisheries management.

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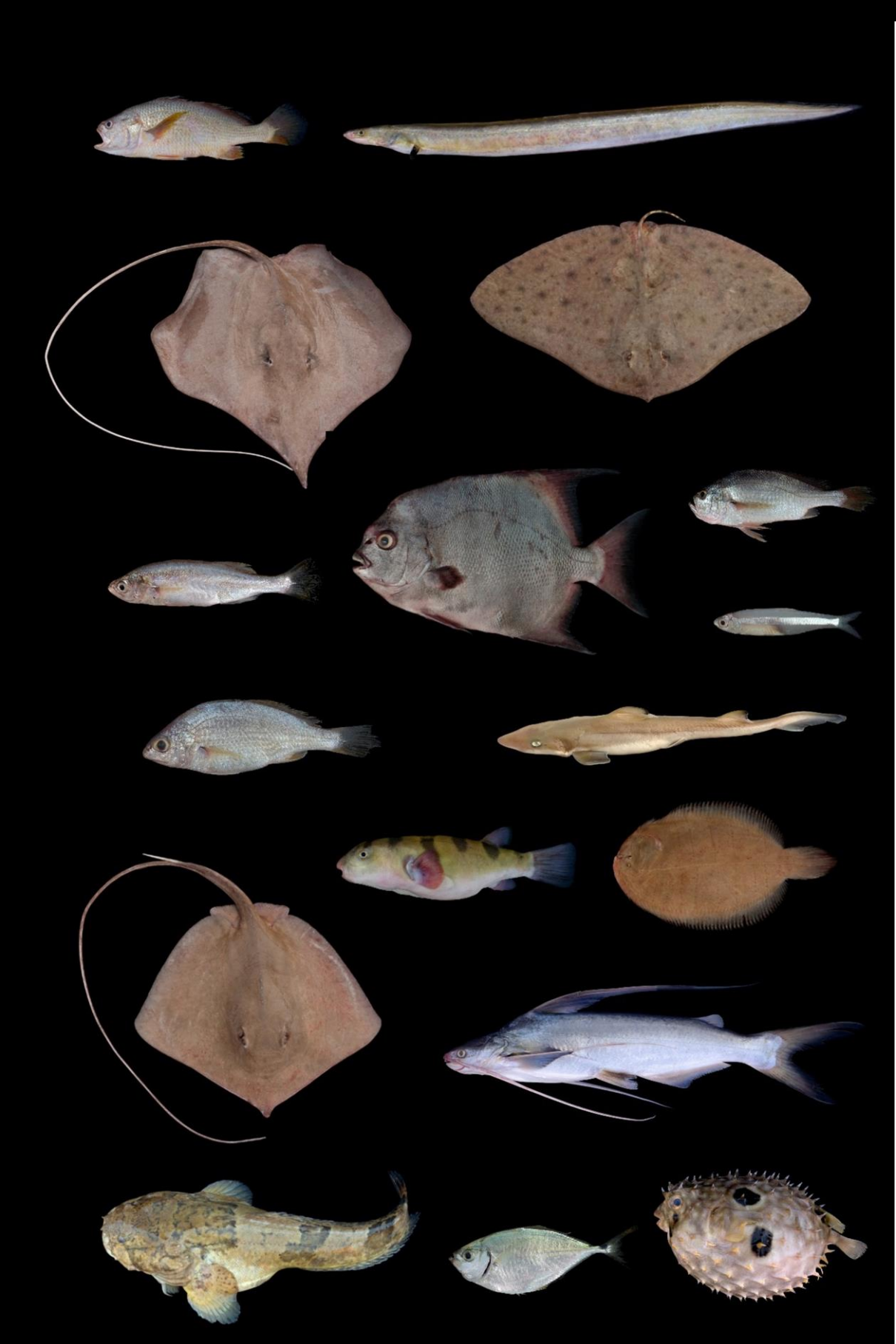

3

DISTRIBUTION PATTERNS OF THE DEMERSAL FISH FAUNA ON THE INNER CONTINENTAL SHELF OF SURINAME

Modified from:

Willems, T., De Backer A., Mol, J.H., Vincx, M., Hostens, K.. 2015. Distribution patterns of the demersal fish fauna on the inner continental shelf of Suriname. Regional Studies in Marine Science 2:177-188.

This study aimed to characterise the spatio-temporal patterns of the demersal fish community in the shallow (<40 m) inner shelf waters of Suriname, based on (bi)monthly data for the period February 2012 - April 2013. From 148 demersal trawl samples, distributed over 15 locations, 98 fish species were identified. Stellifer rastifer, Amphiarius rugispinis *and* Cynoscion jamaicensis *represented 50 % of the catches. Cluster analysis revealed three species assemblages, occurring in a nearshore-offshore depth gradient. A coastal fish assemblage occurred in the shallow turbid waters, characterised by muddy sediments with relatively high organic carbon content. A transition assemblage around 27 m water depth marked the shift towards a very different* offshore *fish assemblage on the deepest sampling locations (34 m), which were characterised by coarser sediments, with clear overlying waters. The* coastal *assemblage represented the 'sciaenid community' of tropical shelves, dominated by Sciaenidae and Ariidae. The* offshore *assemblage had a significantly lower fish density and diversity, and contained representatives of fish families typical for deeper tropical shelves, such as Paralichthyidae, Triglidae and Lutjanidae. The shift between the* coastal *and* offshore *fish assemblage was the most important feature of the demersal fish community, and coincided with a transition between two principal ecosystems: a coastal, river influenced system fuelled by detritus versus an open shelf system based on primary production. Whereas pelagic fishes are known to gain in importance on the open shelf, demersal fishes thrived in the coastal ecosystem, together with a potentially important epibenthic food source, the Atlantic seabob shrimp* Xiphopenaeus kroyeri. *In Suriname, large demersal (mainly sciaenid) fishes are the main fisheries resource for the artisanal fleet in the nearshore waters below 20 m depth. Because juveniles of commercially important fishes were abundant in our coastal trawl catches, we suggest the shallow nearshore waters have a main nursery function*

1 INTRODUCTION

Coastal and shelf ecosystems worldwide provide nursery habitats for commercial fish species, coastal protection, water purification, carbon sequestration and recreational opportunities (Barbier et al., 2011). Biological production in shelf seas supports over 90 % of global fish catches (Pauly et al., 2002), and coastal fisheries generate income, employment and food security for millions of people (UNEP, 2011). While fisheries management has relied on individual fish stock assessments for decades, there is a growing consensus within the Ecosystem Approach to Fisheries (EAF) to consider the ecosystem-wide effects of fishing for a proper management of natural resources (Garcia et al., 2003; Beddington et al., 2007). Because an EAF recognizes the complexity of ecosystem structure and functioning, basic understanding on the occurrence of the different life stages of exploited species and the interactions among them is essential, as well as understanding their relationship with the environment (e.g. Pikitch et al., 2004).

The current study was conducted on the continental shelf of Suriname, located in the Guianan Ecoregion of the North Brazil Shelf (Spalding et al., 2007). The productive coastal waters are highly influenced by heavy river runoff, notably from the Amazon River (Cadée G.C., 1975; Smith and Demaster, 1996), and support extensive artisanal and industrial coastal fisheries (Miloslavich et al., 2011). In Suriname, the shallow nearshore waters below 20 m depth support about 70 % of the total landings. These are mainly caught by artisanal small-scale fisheries, which use gillnets and fyke nets to catch sciaenid fishes (Perciformes: Sciaenidae) and Atlantic seabob shrimp *Xiphopenaeus kroyeri*. Somewhat deeper on the shelf, industrial bottom trawl fisheries targeting *X. kroyeri* are allowed between 18 m – 30 m depth, while trawling for other demersal species like larger penaeid shrimps and finfish is only allowed from 30 m depth onwards (Bhagwandin, 2012).

Despite the socio-economic importance of fisheries on the inner Suriname Shelf, little information is available on the ecology and distribution of the demersal fish fauna. Early surveys were mainly taxonomic (e.g. Boeseman, 1948) or aimed at identifying fisheries resources (Aizawa et al., 1983). Charlier and Babb-Echteld (1994) report on the distribution of shrimp and fishes on the inner shelf based on the latest demersal trawl survey in Suriname (1993-1994). They mention a decrease in demersal finfish yield beyond 30 m, with the bulk of the biomass of commercial species occurring in less than 20 m depth. Because no environmental data were collected during this survey, the ecological interpretation for understanding the distribution patterns was not possible. In the wider Guianan Ecoregion, e.g. in Guyana (Lowe-McConnell, 1962), French-Guiana (Durand, 1959; Guéguen F., 2000; Vendeville and Baudrier, 2006) and between the Orinoco and Maroni River (Bianchi, 1992), differences between a coastal and a more offshore (deeper shelf) fish

assemblage were found, mainly related to differences in sediment characteristics. Similarly, a recent study on the epibenthic (invertebrate) communities of the inner Suriname Shelf (Willems et al., 2015b) showed an nearshore-offshore transition in species assemblages, linked to a gradient in sediment characteristics. In the nearshore waters with muddy Amazon-borne sediments, low epibenthic diversity was encountered, though *Xiphopenaeus kroyeri* reached high densities. Beyond 30 m depth, on coarser sediments, *X. kroyeri* was absent and epibenthic diversity was higher.

In the current study, we investigated the structure and dynamics of the demersal fish community of the inner Suriname Shelf area, which was sampled simultaneously with this epibenthos. The main objective was to provide an ecological context for the demersal fish populations on the inner Suriname Shelf. This was done by identifying species assemblages, their spatio-temporal distribution patterns and by linking their occurrence with both abiotic and biotic environmental parameters. This study is the first in 20 years to provide fisheries-independent information on the occurrence of demersal fish species and length-specific abundances. We compared our results with the knowledge on the fish fauna of the wider Guianan Ecoregion, and discuss how our findings can contribute to an ecosystem approach to fisheries management in Suriname.

2 MATERIALS AND METHODS

2.1 STUDY AREA

The Suriname Shelf (54 – 57 °W, 6 – 7 °N, Fig. 1) is situated in the Guianan Ecoregion of the North Brazil Shelf Province (Spalding et al., 2007). The area is characterised by wide, gently sloping continental shelves, macrotides and upwelling along the shelf edge, and is profoundly influenced by the turbid freshwater discharge from the Amazon River (Heileman, 2008), which is carried to the coast of Suriname by the North Brazil Current and its extension, the Guiana Current (Johns et al., 1998; Hellweger and Gordon, 2002). Shelf waters in the region can generally be characterised by three major zones parallel to the coast (Lowe-McConnell, 1962; Cadée G.C., 1975; Smith and Demaster, 1996). The *brown* nearshore waters have a high turbidity and low salinity due to suspension of the muddy deposits and freshwater input of both the Amazon and main local rivers. Between 20 and 50 km offshore, the combination of riverine nutrient input and decreased turbidity creates a productive zone with high chlorophyll concentrations, termed the *green water zone*. Offshore from this zone irradiance further increases, while nutrients become limited for primary production, causing *blue waters*. Most rainfall in Suriname, and peak discharge of both the Amazon and local rivers, occurs between December and July (Amatali, 1993, Hu et al., 2004). From August to November, the

combination of drier weather and a weaker Guiana Current causes less input of (Amazon) river discharges in the nearshore waters of Suriname. This is also a period with reduced northeast trade winds causing calm and warmer sea surface waters (Amatali, 1993; Augustinus, 2004).

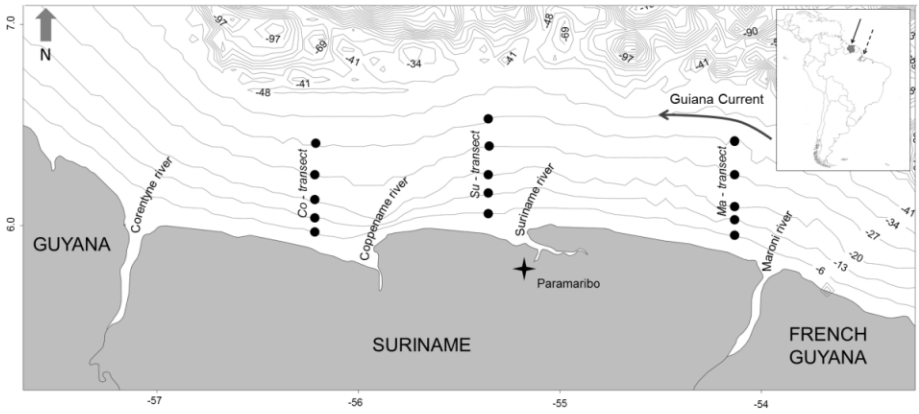

Figure 1. Map of the inner Suriname Shelf with indication of the major river estuaries and the direction of the Guiana Current. Dots represent the sampling sites at 5 depths (6, 13, 20, 27, 34 m) in each of 3 transects: Co-transect in the west, Su-transect in the middle, Ma-transect in the east. Inset indicates the location of Suriname (solid arrow) and the Amazon River estuary in Brazil (dashed arrow).

2.2 SAMPLING AND DATA ORIGIN

Data originated from 10 trawl surveys for epibenthos and demersal fish conducted between February 2012 and April 2013 (see Willems et al., 2015b). Fifteen locations on the inner shelf were sampled onboard Neptune-6, a 25-m long commercial outrigger trawler used in the Suriname Atlantic seabob shrimp *Xiphopenaeus kroyeri* trawling fleet. A small otter trawl at the stern of the vessel (the 'try-net': 4.3 m horizontal spread; 45 mm stretched cod end mesh size) was used for sampling. This gear type was chosen because it is known to operate well on the often muddy seabed, and it has proven efficient in catching epibenthos and demersal fish. All stations were sampled monthly for the first 6 months and bi-monthly later on (Table 1). Sampling locations were situated along three North-South transects positioned near the westward directed outflow of the Coppename (Co), Suriname (Su) and Maroni (Ma) rivers (Fig. 1). Each transect consisted of five locations along a depth gradient (6, 13, 20, 27 and 34 meters depth). Sampling was done onboard Neptune-6, a 25-m long commercial outrigger trawler used in the Suriname Atlantic seabob shrimp *Xiphopenaeus kroyeri* trawling fleet. At each location, the net was towed for 40 minutes in westward direction at a speed of approximately 2.5 knots. Sampling time, start and stop coordinates and sampling depth were noted to enable a correct conversion towards sampled surface units. Upon retrieval of the trawl, all fishes were sorted from the catch, identified and measured to the nearest cm (total length for finfish, disc width for rays). Species identification

was based on Aizawa et al. (1983), Cervigón et al. (1993) and Léopold (2005). Fish names followed Eschmeyer (2015) and higher classification was according to Nelson (2006).

For each trawl sample, water clarity (*Secchi*-depth) and sub-surface (5 m depth) total suspended matter (SS-TSM) was measured. Due to logistic problems, CTD-data on water salinity, temperature and depth were only gathered for the first six campaigns. During three campaigns (February, April and May 2012) bottom sediment samples were collected with a Van Veen grab to assess sediment characteristics, including median grain size of the sand fraction (63-2000 μm; MEDSAND), mud-content (<63 μm; MUD) and total organic carbon content (TOC). These *in-situ* environmental data were complemented by remote-sensing values on surface total suspended matter concentrations (SF-TSM), chlorophyll *a* concentrations (CHL) and sea surface temperature (SST) from the satellite-borne sensor MODIS on the polar-orbiting Aqua satellite (OBPG, 2014; Bailey et al., 2010). Land rainfall and river discharge data for Maroni river and Amazon river were available from the Suriname Meteorological Service and the Environmental Research Laboratory (ORE-HYBAM, 2014), respectively. Detailed data on the spatio-temporal distribution patterns in the epibenthos, the detailed description of the abiotic parameters, and more details on the density *Xiphopenaeus kroyeri*, the most abundant epibenthic species in the study area, are presented in Willems et al. (2015b). In the current study, these data are used as explanatory environmental variables, hence their collection and analyses is not further described here.

Table 1. Overview of date and season of each sampling campaign (more details on abiotic parameter measurements in Willems et al. (2015b)).

Nr	Date	Season
1	17/02 - 22/02/2012	rainy
2	24/03 - 29/03/2012	rainy
3	20/04 - 25/04/2012	rainy
4	22/05 - 29/05/2012	rainy
5	30/06 - 04/07/2012	dry
6	21/07 - 26/07/2012	dry
7	29/09 - 04/10/2012	dry
8	27/11 - 01/12/2012	dry
9*	29/01 - 03/02/2013	dry
10**	10/04 - 15/04/2013	rainy

* missing data for location Ma06

**missing data for location Ma34

2.3 DATA ANALYSIS

Sampling campaigns were considered to occur either in *rainy* or *dry* season based on real-time river outflow data of Maroni River with a cut-off at the mid-range discharge value (2960 $m^3.s^{-1}$). As such, the campaigns in February, March, April and May 2012 were considered as *rainy* (Table 1). The five following campaigns were *dry* while the last campaign (April 2013) was again *rainy.*

Pelagic fish species (following FishBase) (Froese and Pauly (Eds.), 2014) in the samples were excluded from all analyses as they were not sampled quantitatively with the demersal otter trawl. Fish abundance data were standardized, and expressed as numbers per surface unit (1000 m^2). For the most abundant demersal fish species, length-frequency distributions (LFD) were explored graphically and compared to the *common length,* i.e. the size at which fish specimens are commonly caught or marketed according to FishBase (Froese and Pauly (Eds.), 2014). For every sample, species richness (S), total density (N) and Shannon diversity index (H') was calculated on the full demersal fish species matrix (excluding pelagic species) using the DIVERSE function in PRIMER v6 (Clarke and Gorley, 2006).

Multivariate analyses were performed on fourth-root transformed fish abundance data using the Bray-Curtis similarity index with further exclusion of rare demersal fish species (occurring in <3 % of the samples) to reduce the influence of highly abundant and rare fish species, respectively. Distance-based linear models (DistLM) using BEST selection and BIC criterion were used to relate patterns in species composition and abundance to environmental variables (Anderson et al., 2008). Environmental data were normalized and collinearity among all variables was examined using Spearman rank correlation coefficients prior to the DistLM analyses. For linear dependent variables ($|r| \geq 0.8$) only one variable was retained in the analyses. Depth, MUD, *Secchi*-depth, rainfall and total epibenthic density were excluded from the DistLM analyses due to collinearity with respectively TOC (first three), Maroni discharge and density of *Xiphopenaeus kroyeri*. As such CHL, SF-TSM, SS-TSM, SST, Maroni discharge, Amazon discharge, MEDSAND, TOC and (fourth-root transformed) density of *X. kroyeri* were included in the analyses. As sediment was only three times sampled, averages per location were calculated from these campaigns, and used for the missing months (this approach was validated by a DistLM analyses with only the three campaigns, giving similar results as the full DistLM analyses).

A cluster analysis with SIMPROF tests (significance level 1 %) was conducted to investigate the fish community structure (Clarke and Gorley, 2006). The significance level was set more stringent given the multiple testing inherent in this hierarchical approach as suggested in Clarke et al. (2008). Next, a SIMPER analysis (cut-off 90%) was performed to determine the species that characterised each species assemblage as identified by the cluster analysis.

Assemblages were further characterised in terms of average density (N) and diversity (species richness S, Shannon diversity index H'), and the most relevant (DistLM-based) environmental variables. Significant differences in these univariate parameters between assemblages were tested through one-way Permanova analyses, based on the Euclidean distance resemblance matrix with unrestricted permutation of raw data (Anderson et al., 2008) and through pairwise tests when significant differences were found. Monte Carlo corrections were applied when too few (<100) permutations could be calculated (Anderson and Robinson, 2003). Further, species richness (with the inclusion of rare demersal species) was compared among assemblages by means of species-accumulation curves (e.g. Gotelli and Colwell, 2001) with random permutation of the samples. Environmental characteristics of the assemblages were visualized by overlaying the most important parameters (based on DistLM) as vectors on a non-metric multi-dimensional scaling (nMDS) plot of the samples using multiple correlation (Clarke and Gorley, 2006).

Within-assemblage patterns in species composition and abundance were investigated for small-scale spatial and temporal patterns, using a three-way Permanova design with the factors 'depth', 'transect' and 'season'. These analyses were based on a Bray-Curtis similarity index constructed of fourth-root transformed species abundance data for all samples per identified cluster. Finally, within-assemblage variation in the univariate parameters was tested using a similar three-way Permanova design based on an Euclidean distance resemblance matrix.

All data analyses were performed in R v.3.0.1 (R Core Team, 2013) and in PRIMER v.6.1.13 with Permanova add-on software (Clarke and Gorley, 2006; Anderson et al., 2008). A significance level of p=0.05 was used in all tests. Throughout the text, averages are always given together with their standard deviation (SD).

3 RESULTS

3.1 GENERAL CHARACTERISATION OF THE FISH COMMUNITY

From the 148 otter trawl samples, 18892 fishes were collected and 98 fish taxa were identified, most of them to species level and hereafter referred to as species (Table 2). Fish species belonged to 47 families and 14 orders with Perciformes (46 species) and Siluriformes (13 species) being dominant. Thirteen pelagic fish species were excluded from all further analyses (Table 2). Samples contained between 3 and 24 demersal fish species with an average of 11.4 ± SD 4.1 species per sample. Total fish density at the sampling stations averaged 9.7 ± 8.5 ind.1000 m^{-2}, and ranged from 0.7 to 62.1 ind.1000 m^{-2}. Ten

species accounted for 83 % of all fishes caught, while the three most abundant species, *Stellifer rastifer, Amphiarius rugispinis* and *Cynoscion jamaicensis* accounted for 50 % of the catches. These three species, together with *Dasyatis guttata, Macrodon ancylodon* and *Stellifer microps* were also prevalent most consistently, occurring in more than half of the samples. Many species were rare: 13 species were found in a single sample, while 28 species occurred in less than 3 % of the samples (Table 2).

The most abundant fish species generally had unimodal length-frequency distributions (LFD), with a peak between 7 and 15 cm total length. *Amphiarius rugispinis* showed a bimodal distribution, while length (disc width) of the two abundant ray species *Gymnura micrura* and *D. guttata* spanned a large range (Fig. 2). When comparing the LFD with literature data, the reported *common length* matched with the peak of the LFD only in the small sciaenid *Stellifer microps*. All other species were smaller than the *common length,* notably the stingrays *D. guttata* and *G. micrura* (Fig. 2).

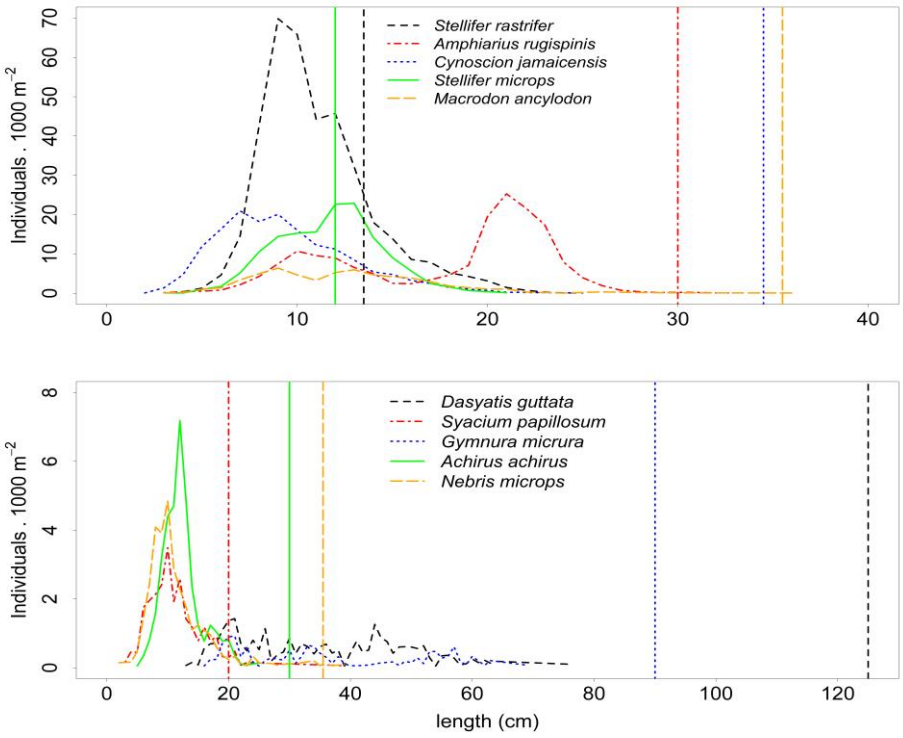

Figure 2. Length-frequency distributions of the 10 most abundant fish species. Vertical lines indicate the reported *common lengths* for each species (based on FishBase). Note the different axis scales on both plots to account for variation in fish abundance and length.

Table 2. Fish taxa identified from the trawl samples. n = total number of specimens collected in 148 trawl samples.

Order	Family	Species	n
Albuliformes			
	Albulidae	*Albula vulpes***	1
Anguilliformes			
	Muraenesocidae	*Cynoponticus savanna*	10
	Nettastomatidae	*Hoplunnis sp.**	16
	Ophichthidae	*Ophichthus cylindroideus**	1
Aulopiformes			
	Synodontidae	*Saurida caribbaea*	41
		Synodus foetens	32
		*Trachinocephalus myops**	1
Batrachoidiformes			
	Batrachoididae	*Batrachoides surinamensis*	23
		*Porichthys plectrodon**	2
Carcharhiniformes			
	Triakidae	*Mustelus higmani*	9
Clupeiformes			
	Clupeidae	*Harengula jaguana*	59
	Engraulidae	*Anchoa spinifer***	132
		*Anchovia surinamensis***	8
		*Anchoviella lepidentostole***	25
		*Pterengraulis atherinoides***	10
	Pristigasteridae	*Odontognathus mucronatus***	247
		*Pellona flavipinnis***	39
Lophiiformes			
	Ogcocephalidae	*Ogcocephalus sp.*	19
Perciformes			
	Carangidae	*Caranx hippos***	2
		*Chloroscombrus chrysurus***	54
		*Oligoplites saliens**	1
		Selene brownii	42
		Selene vomer	13
		*Trachinotus cayennensis**	6
		*Carangidae sp.***	3
	Centropomidae	*Centropomus ensiferus*	15
		*Centropomus parallelus**	1
	Ephippidae	*Chaetodipterus faber*	26
	Gerreidae	*Diapterus auratus**	2
	Gobiidae	*Gobionellus oceanicus**	1
	Haemulidae	*Conodon nobilis**	6
		Genyatremus luteus	5
	Sciaenidae (cont.)	*Lonchurus elegans*	89
		Lonchurus lanceolatus	58
		Macrodon ancylodon	841
		Menticirrhus americanus	56
		Micropogonias furnieri	19
		Nebris microps	440
		Paralonchurus brasiliensis	203
		*Plagioscion auratus**	4
		Stellifer microps	2094
		Stellifer rastrifer	5451
	Scombridae	*Scomberomorus brasiliensis***	1
	Serranidae	*Diplectrum formosum*	22
		Diplectrum radiale	67
	Sparidae	*Calamus penna**	1
	Stromateidae	*Peprilus paru*	27
	Trichiuridae	*Trichiurus lepturus***	71
Pleuronectiformes			
	Achiridae	*Achirus achirus*	480
		Apionichthys dumerili	55
	Bothidae	*Bothus ocellatus**	3
	Cynoglossidae	*Symphurus plagusia*	133
	Paralichthyidae	*Syacium papillosum*	347
Rajiformes			
	Dasyatidae	*Dasyatis americana**	3
		Dasyatis geijskesi	35
		Dasyatis guttata	390
	Gymnuridae	*Gymnura micrura*	190
	Myliobatidae	*Rhinoptera bonasus**	1
	Rhinobatidae	*Rhinobatos percellens**	5
	Urotrygonidae	*Urotrygon microphthalmum*	77
Scorpaeniformes			
	Dactylopteridae	*Dactylopterus volitans*	13
	Scorpaenidae	*Scorpaena sp.*	11
	Triglidae	*Prionotus punctatus*	282
Siluriformes			
	Ariidae	*Amphiarius phrygiatus**	55
		Amphiarius rugispinis	2540
		Aspistor quadriscutis	115
		Bagre bagre	56
		Notarius grandicassis	18

Table 2. continued.

Order	Family	Species	n	Order	Family	Species	n
		Haemulon boschmae	66			*Sciades couma**	1
		Orthopristis ruber	136			*Sciades herzbergii**	2
		Pomadasys corvinaeformis	12			*Sciades parkeri*	4
	Lutjanidae	*Lutjanus jocu**	1			*Sciades passany**	3
		*Lutjanus purpureus**	1			*Sciades proops**	3
		Lutjanus synagris	73		Aspredinidae	*Aspredo aspredo**	7
	Mullidae	*Upeneus parvus*	29		Auchenipteridae	*Pseudauchenipterus nodosus**	2
	Polynemidae	*Polydactylus oligodon*	14	**Tetraodontiformes**			
		*Polydactylus virginicus**	2		Diodontidae	*Chilomycterus antillarum*	6
	Priacanthidae	*Priacanthus arenatus*	16		Monacanthidae	*Stephanolepis hispidus**	6
	Sciaenidae	*Ctenosciaena gracilicirrhus*	344		Ostraciidae	*Acanthostracion quadricornis*	5
		Cynoscion jamaicensis	2340		Tetraodontidae	*Colomesus psittacus*	123
		Cynoscion microlepidotus	5			*Lagocephalus laevigatus***	3
		Cynoscion virescens	276			*Sphoeroides testudineus*	9
		*Isopisthus parvipinnis**	1	**Torpediniformes**			
		Larimus breviceps	233		Narcinidae	*Narcine bancoftii*	64

** = rare (present in < 3 % of samples); ** = pelagic species (according to FishBase)*

3.2 ENVIRONMENTAL INFLUENCE AND FISH ASSEMBLAGE STRUCTURE

Based on the defined criteria (demersal and present in >3 % of all samples), 58 of the 98 fish species were retained for multivariate analyses (Table 2).

The linear combination of environmental variables that best explained the variation in the multivariate data cloud included MEDSAND (37 %), TOC (49 %), SS-TSM (9 %) and density of *Xiphopenaeus kroyeri* (45 %) (marginal tests). When fitted together, these variables explained 37 % of the total variation in the fish community structure (DistLM BEST – BIC).

Hierarchical clustering of the samples revealed three main clusters. A first cluster split off at ca. 10 % similarity, containing mainly 34m-samples and as such termed the *offshore assemblage* (Fig. 3). At a 30 % similarity level, the other two clusters and two outliers were discerned. The largest cluster mainly grouped samples from the 6, 13 and 20 m depth zones, and is further referred to as the *coastal assemblage*. A smaller cluster with mainly 27m-samples can be regarded as the *transition assemblage* (Fig.3 & 4).

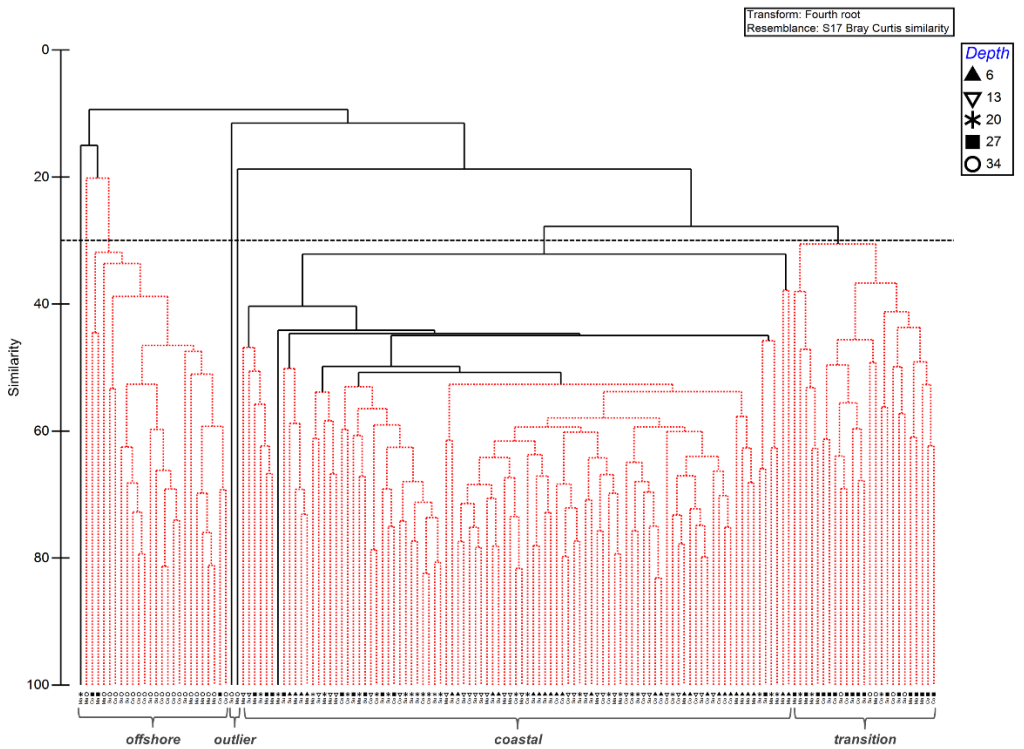

Figure 3. Group-averaging cluster analysis based on Bray-Curtis resemblance matrix of fourth-root-transformed species abundance data in all fish samples. Significant clusters (SIMPROF test 1 % significance level) are indicated by the coloured (red) lines. Samples are labeled with depth (symbol) and transect (Ma=Marowijne transect; Su=Suriname transect; Co=Coppename transect). The dashed line indicates the 30 % similarity level.

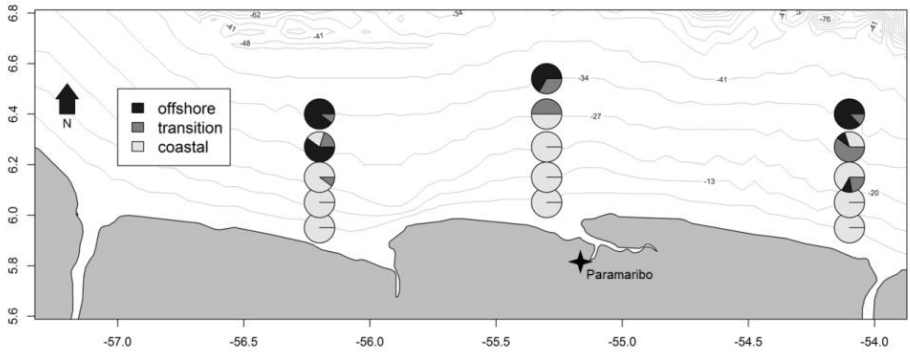

Figure 4. Map of the fish species assemblages as identified by cluster analysis. Each pie represents the allocation of the different fish samples collected at a station (n=9 or 10) to an assemblage. Two outlier samples are not considered.

3.3 CHARACTERISATION OF THE ASSEMBLAGES

One-way SIMPER analysis showed that the *coastal assemblage* had an average similarity of 51 %, and mainly consisted of sciaenid fishes (Perciformes: Sciaenidae) including *Stellifer rastifer*, *S. microps*, *Cynoscion jamaicensis* and *Macrodon ancylodon*. The catfish *Amphiarius rugispinis* (Siluriformes: Ariidae) was also characteristic for the *coastal assemblage* (Table 3). With 61 demersal fish species identified, the *coastal assemblage* was the most diverse. The *offshore assemblage* was characterised by less (i.e. 39), and very different species, with *Syacium papillosum* (Pleuronectiformes: Paralichthyidae), *Dasyatis guttata* (Rajiformes: Dasyatidae) and *Prionotus punctatus* (Scorpaeniformes: Triglidae) being the most important contributors to the average within-group similarity of 42 %. The transition assemblage was a less well-defined species assemblage with the lowest average similarity (38 %). It was characterised by a mix of 49 *coastal* and *offshore* species, although still dominated by Sciaenidae (Table 3, Fig. 5).

Significant differences between the three assemblages were observed for total fish density (Pseudo-F=11.0; p=0.0001), species richness (Pseudo-F=37.7; p=0.0001) and Shannon diversity (Pseudo-F=47.7; p=0.0001). Fish density (N) in the *coastal assemblage* was significantly higher than in the *transition* and *offshore assemblage*. Species richness (S) significantly decreased from *coastal* to *offshore,* while Shannon diversity (H') was significantly lower in the *offshore* compared to the *coastal* and *transition assemblage* (pairwise tests; Table 3; Fig.6). Correcting for sampling effort, the species-accumulation curve for each assemblage also showed the lowest diversity of demersal fishes in the *offshore assemblage* (Fig. 7).

Table 3. Characterisation of the three species assemblages as defined by hierarchical cluster analysis, showing average 'within-group' similarity based on one-way SIMPER analysis of fourth-root transformed abundance data. Species accounting for 90 % cumulative contribution of the 'within group' similarity are listed along with their contribution (%) and average density (N; ind.1000 m^{-2}). The average (± SD) per assemblage for a number of univariate parameters is also given. MEDSAND = median grain size of the sand faction, TOC = sediment total organic carbon, SS-TSM = sub-surface total suspended matter, *X. kroyeri* = density of the Atlantic seabob shrimp *Xiphopenaeus kroyeri*

Coastal assemblage (avg. sim.= 50.7)			Transition assemblage (avg. sim.= 38.5)			Offshore assemblage (avg. sim.= 41.6)		
Species	**%**	**N**	**Species**	**%**	**N**	**Species**	**%**	**N**
Stellifer rastrifer Rake stardrum	17	4.05	*Cynoscion jamaicensis* Green weakfish	25	1.43	*Syacium papillosum* Dusky flounder	39	2.76
Amphiarius rugispinis Softhead sea catfish	15	1.84	*Dasyatis guttata* Longnoze stingray	18	0.88	*Dasyatis guttata* Longnoze stingray	18	0.35
Cynoscion jamaicensis Jamaica weakfish	10	1.33	*Ctenosciaena gracilicirrhus* Barbel drum	10	0.96	*Prionotus punctatus* Bluewing searobin	18	0.37
Macrodon ancylodon King weakfish	9	0.55	*Prionotus punctatus* Bluewing searobin	9.1	0.35	*Lutjanus synagris* Lane snapper	7.3	0.16
Stellifer microps Smalleye stardrum	8	1.24	*Paralonchurus brasiliensis* Banded croaker	5.6	0.27	*Diplectrum radiale* Pond perch	5.4	0.18
Dasyatis guttata Longnoze stingray	7	0.53	*Stellifer microps* Smalleye stardrum	4.6	1.05	*Synodus foetens* Inshore lizardfish	3.9	0.07
Gymnura micrura Smooth butterfly ray	6.2	0.38	*Orthopristis ruber* Corocoro grunt	4.2	0.18			
Nebris microps Smalleye croaker	5.7	0.34	*Menticirrhus americanus* Southern kingcroaker	4.2	0.11			
Cynoscion virescens Green weakfish	5.1	0.19	*Larimus breviceps* Shorthead drum	3.6	0.24			
Achirus achirus Drab sole	4.9	0.38	*Symphurus plagusia* Duskycheek tonguefish	2.4	0.05			
Symphurus plagusia Duskycheek tonguefish	2.1	0.08	*Gymnura micrura* Smooth butterfly ray	2.2	0.15			
Urotrygon microphthalmum Smalleyed round stingray	1.4	0.17	*Stellifer rastrifer* Rake stardrum	1.7	0.16			

N samples	95	25	26
Density (ind.1000 m^{-2})	12.0 ± 9.2	6.8 ± 4.7	4.7 ± 4.7
Species richness S	12.6 ± 3.3	10.4 ± 3.4	6.5 ± 2.8
Shannon diversity H'	1.8 ± 0.3	1.7 ± 0.3	1.2 ± 0.3
Depth (m)	15.9 ± 8.3	30.6 ± 5.1	37.3 ± 5.3
MEDSAND (μm)	121.8 ± 50.2	225.7 ± 94.2	288.8 ± 97.9
TOC (%)	1.1 ± 0.2	0.6 ± 0.3	0.4 ± 0.1
SS-TSM (g.m^{-3})	62.6 ± 40.7	38.9 ± 14.3	38.3 ± 12.0
***X. kroyeri* (ind. 1000 m^{-2})**	152.5 ± 191.4	106.8 ± 280.9	0.0 ± 0.0

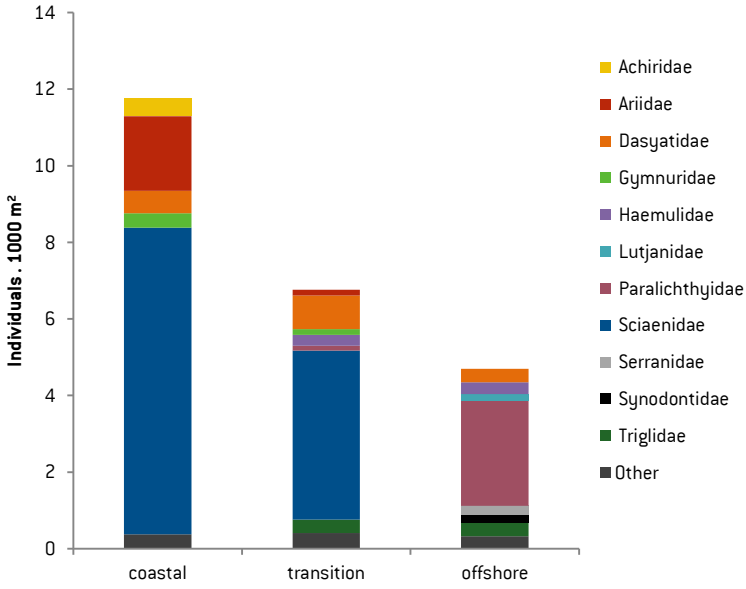

Figure 5. Barplots showing average fish density per assemblage broken down in the main contributing fish families.

Fish assemblages also differed in environmental parameters: Depth (Pseudo-F=69.4; p=0.0001), MEDSAND (Pseudo-F=68,5; p=0.0001), TOC (Pseudo-F=131.0; p=0.0001) and SS-TSM (Pseudo-F=8.3; p=0.001). Pairwise comparisons revealed a significant *coastal* to *offshore* increase in depth and MEDSAND, while TOC showed the opposite trend. SS-TSM was significantly higher in the *coastal assemblage* compared to the other assemblages. *Xiphopenaeus kroyeri* was absent from the offshore assemblage, whereas densities did not differ between the *coastal* and *transition assemblage* (pairwise tests; Fig.6). The influence of (DistLM-selected) environmental parameters on fish community structure was visualized by overlaying them as vectors in the nMDS plot (Fig. 8).

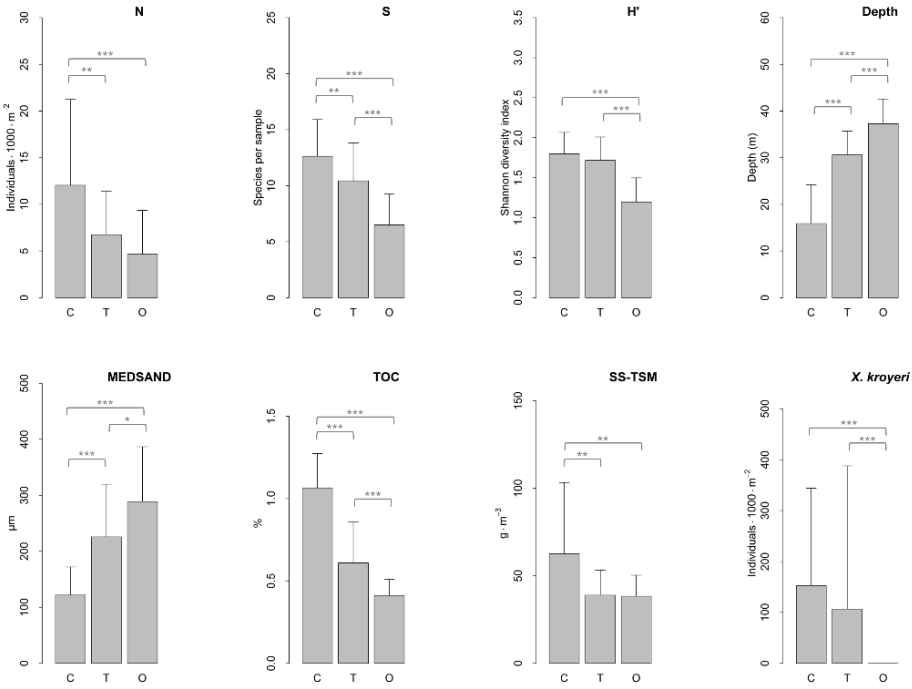

Figure 6. Barplots showing main characteristics (averages + SD) of the 3 assemblages (C=*coastal*, T=*transition*, O=*offshore assemblages*). N=total fish density, S=species richness, H'=Shannon-diversity, MEDSAND = median grain size of the sand faction, TOC = sediment total organic carbon, SS-TSM = sub-surface total suspended matter, *X. kroyeri* = density of the Atlantic seabob shrimp *Xiphopenaeus kroyeri.* Significant differences between communities as defined by Permanova are indicated (*p=0.01-0.05, **p=0.001-0.01, ***p<0.001).

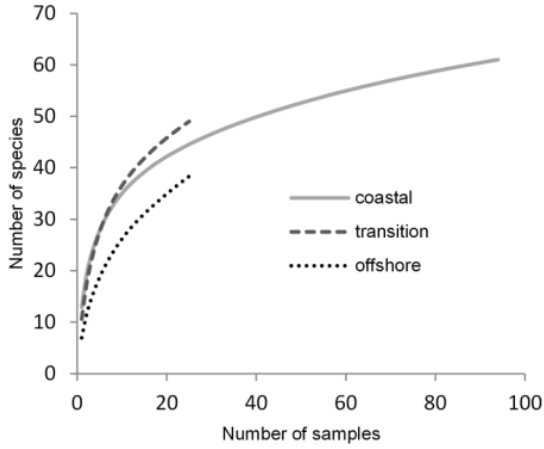

Figure 7. Species accumulation curves showing the number of demersal fish species encountered in a number of randomly permutated samples.

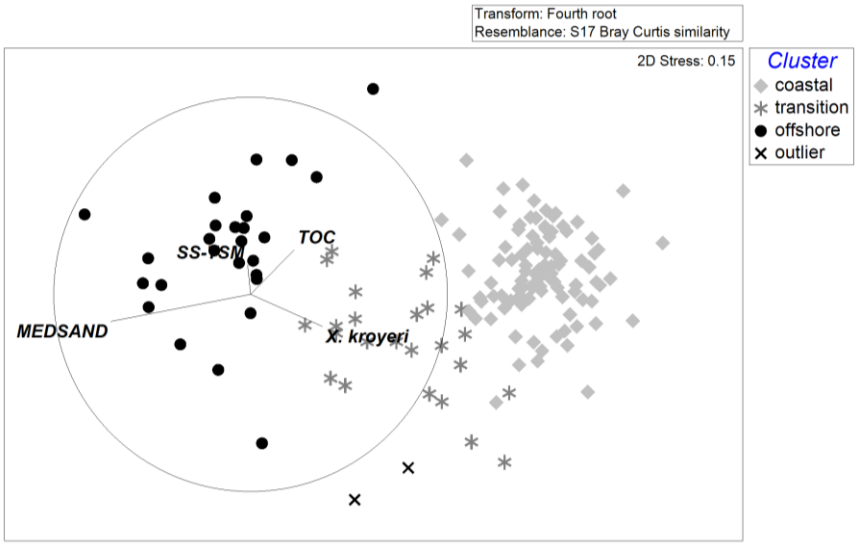

Figure 8. Non-metric multidimensional scaling (nMDS) ordination plot based on Bray-Curtis resemblance matrix of fourth-root-transformed species abundance data of all fish samples. Each symbol represents one trawl sample. Symbols represent species assemblages delineated from hierarchical clustering. The four environmental variables selected to fit the best model in DistLM are overlaid as vectors using multiple correlation. TOC = sediment total organic carbon; MEDSAND = median grain size of the sand faction; SS-TSM = sub-surface total suspended matter; *X. kroyeri* = density of the Atlantic seabob shrimp *Xiphopenaeus kroyeri.*

Looking at a more detailed level within each assemblage, no significant spatial or temporal patterns in species composition and abundance, total fish density, species richness or Shannon diversity were apparent in the *transition assemblage*. In the *coastal assemblage*, however, significant spatial (depth x transect interaction, Pseudo-F=2.2; p=0.0001) and temporal (season effect, Pseudo-F=2.0; p=0.0346) differences in species composition and abundance were observed (Annex 3.1). Pairwise tests in the depth x transect interaction revealed significant differences among depths in each transect, and among transects at most depths (pairwise tests; Annex 3.1). Two-way SIMPER analysis (depth x transect) revealed little spatial variation in the abundances of the typical *coastal* species, but tests of the univariate parameters showed significantly higher total fish density in the Co-transect (17.6 ± 11.8 ind.1000m^{-2}) compared to the Su- (9.7 ± 5.9 ind.1000m^{-2}) and Ma-transect (8.9 ± 6.3 ind.1000m^{-2}; Annex 3.2). No significant seasonal effects were found in any of the univariate parameters within the *coastal assemblage*, nor did one-way SIMPER reveal obvious differences in species composition between the *rainy* and *dry* season. Finally, within the *offshore assemblage* species composition and abundance differed between the *rainy* and *dry* season (Pseudo-F=2.0; p=0.0449), mainly caused by higher abundances in the *rainy* season (one-way SIMPER). Univariate tests also showed a higher species richness in the *rainy* compared to the *dry* season (resp. 8.0 ± 3.4 *vs.* 5.4 ± 1.5 species per sample; Annex 3.2). No spatial patterns were found within the *offshore assemblage*.

4 DISCUSSION

4.1 SPATIO-TEMPORAL PATTERNS IN THE DEMERSAL FISH COMMUNITY OF THE INNER SURINAME SHELF

The most apparent characteristic of the demersal fish community on the inner Suriname Shelf was a transition from a *coastal* to an *offshore* assemblage around 30 m depth, corresponding with an environmental shift from a shallow environment with muddy deposits rich in organic carbon and turbid overlying waters ('brown-water zone') towards the deeper shelf, which is characterised by coarser sediments and clear waters ('blue water zone'; Lowe-McConnell, 1962). This environmental shift has also been observed in Guyana (Lowe-McConnell, 1962) and French-Guiana (e.g. Vendeville and Baudrier, 2006), and is the main feature structuring demersal assemblages of fishes and invertebrates (up to 200 m depth) between the Orinoco and the Maroni River (Bianchi, 1992). Although the depth range of the current study was limited (6 to 34 m depth), we did observe a shift towards the offshore fish communities of the deeper shelf. Despite some smaller scale spatial and temporal variation within the *coastal* and *offshore* assemblage, the nearshore-offshore spatial gradient remained the most important feature of the demersal fish community.

Both the *coastal* and *offshore* assemblages represented typical fish assemblages that occur in similar habitats throughout the Guianan Ecoregion. Rather than a separate and well-defined assemblage, the *transition assemblage* had characteristics intermediate between the *coastal* and *offshore assemblage,* though it generally resembled the *coastal assemblage* in species composition. The *coastal assemblage* was present in the nearshore waters up to 20 - 27 m depth, and was dominated by drums & croakers (Sciaenidae), but also included catfishes (Ariidae) and stingrays (Dasyatidae, Gymnuridae). This assemblage clearly represents the 'sciaenid community' of tropical shelves, occurring on nearshore and estuarine muddy habitats with turbid waters, from the southern Caribbean to Cape Frio in Brazil (23°S), and in similar environments throughout the tropics (Longhurst and Pauly, 1987). Although most references for the occurrence of sciaenid communities in South-America come from Brazil (e.g. Rocha and Rossi-Wongtschowski, 1998; Bernardes Junior et al., 2011, and references in Rodrigues-Filho et al., 2015), sciaenids also dominated nearshore catches in trawl surveys off Guyana (Lowe-McConnell, 1962; Lowe-McConnell, 1966) and French-Guiana (Durand, 1959; Guéguen, 2000b; Vendeville and Baudrier, 2006). In Guyana, Lowe-McConnell (1966) identified two subsets of the sciaenid community. In the shallowest, turbid nearshore waters over very soft mud, which is in constant suspension and where large changes in salinity occur, sea catfishes (Ariidae) played an important role, while sciaenids became relatively more important when going deeper. In French-Guiana too, 11 of the 17 species of the Ariidae were only found below 10 m depth (Durand, 1959).

Ariidae are known to prefer shallow and low saline estuarine waters and coastal lagoons (e.g. Yanezarancibia and Laradominguez, 1988). Our survey, with the shallowest sampling location around 6 m depth, probably missed a part of this habitat, and therefore we were not able to discriminate a separate catfish-dominated assemblage. We did, however, identify 10 species of Ariidae, some of them very abundant in the *coastal assemblage*.

At the 34 m stations, characterised by coarser sediments with low organic carbon content and rather clear overlying waters, an *offshore assemblage* was discerned, discriminated by the absence of Sciaenidae. Typical fish families in the *offshore* assemblage were Haemulidae, Lutjanidae, Synodontidae and Triglidae, with the dominant species being dusky flounder *Syacium papillosum* (Paralichthyidae). As such, the *offshore assemblage* contained representatives from two tropical western Atlantic fish communities as identified by Longhurst and Pauly (1987): the 'Sparid' (sea bream) community of (muddy) sands and the 'Lutjanid' (snapper) community of rocks, corals and coral sands. The substratum at the *offshore* sampling locations was sandy, explaining the occurrence of a Sparid community. Hard substrate in the form of relict (fossil) coral reefs is also known to occur deeper on the Suriname Shelf (Nota, 1967, also see fig. 1), supporting the presence of a Lutjanid community as well.

Little temporal variation was detected in the fish community, despite clear seasonality in several environmental parameters during the study, e.g. elevated sub-surface total suspended matter and chlorophyll *a* concentrations during the *rainy* season (Willems et al., 2015b). Seasonal patterns were however observed in older studies from Guyana (Lowe-McConnell, 1962) and French Guiana (Puyo, 1949), were a general inshore movement of demersal fishes during the rainy season occurred, most likely related to spawning. On the other hand, Longhurst & Pauly (1987) suggest that within tropical coastal marine ecosystems, interannual changes in species composition and relative abundance are more important than seasonal changes. Further research should clarify to what extent seasonal patterns occur in the demersal fish assemblages on the Suriname Shelf, as insights on (spawning-related) migrations might be relevant for fisheries management.

Spatio-temporal patterns in demersal fish species composition and abundance were related to characteristics of the sediment (MEDSAND and TOC) and water turbidity (SS-TSM). Due to technical problems, our CTD-data were incomplete and could not be included in the DistLM model (see Willems et al., 2015b). As such, while variability in temperature and salinity of the (bottom) water is likely to have an influence on fish distribution as well (e.g.Jaureguizar et al., 2004), this could not be evaluated in the present study.

4.2 LINK BETWEEN DEMERSAL FISH AND EPIBENTHOS ASSEMBLAGES

The shift between *coastal* and *offshore* fish assemblages marks the transition between two principal ecosystems as identified by Bianchi (1992): a coastal, river influenced system fuelled by detritus and characterised by muddy deposits and turbid waters, versus an open shelf system with clear waters and coarser sediment which is based on primary production. This shift seems to have contrasting effects on the diversity of two important ecosystem components on the Suriname Shelf, namely epibenthos and demersal fish. The epibenthic community in the shallow nearshore waters is species poor, but characterised by high densities of the Atlantic seabob shrimp *Xiphopenaeus kroyeri* (Willems et al., 2015b). Except for this shrimp, the estuarine-like conditions in the shallow nearshore waters seem to be too harsh for most epibenthos species, due to rapid environmental changes (Elliott and Quintino, 2007). Average density of *X. kroyeri* formed one of the major structuring variables for the demersal fish community, and *X. kroyeri* might also constitute an important food source for demseral (sciaenid) fishes (e.g. Camargo and Isaac, 2004; Quilez, 2014). This can explain why both density and diversity of demersal fishes was highest in the nearshore waters (*coastal* and *transition* assemblage). The same pattern was noted in other studies from the Guianan Ecoregion (e.g. Lowe-McConnell, 1966; Bianchi, 1992b).

X. kroyeri was almost absent from the *offshore assemblage*, but overall epibenthos diversity increased when progressing offshore on the Suriname Shelf (Willems et al., 2015b). A similar diversity pattern in the epibenthic community was noted in French Guiana (e.g. Le Loeuff and Cosel, 2000), but also in temperate areas like the North Sea (Callaway et al., 2002b). On the contrary, the offshore demersal fish assemblage was characterised by a low diversity and density. Offshore areas are generally characterised by sandy deposits beyond the influence of coastal mud, leading to clearer waters and an increased abiotic stability (Elliott and Quintino, 2007). As such, these offshore areas become less important for demersal fishes. Indeed, Longhurst and Pauly (1987) showed that on tropical shelves, pelagic fishes become relatively more dominant when going offshore.

4.3 CONSIDERATIONS FOR FISHERIES MANAGEMENT IN SURINAME

Several *coastal* fish species that were found to be abundant in our study, such as the sciaenids *Macrodon ancylodon*, *Cynoscion jamaicensis*, *Nebris microps and Cynoscion virescens,* are important target species (as adults) for artisanal gillnet fisheries in Suriname (LVV, 2013). Length-frequency distributions of these and other common species indicated that most fishes were considerably smaller than the common landing lengths (as reported in FishBase), suggesting

that we mainly caught juveniles. This confirms the role of the shallow, estuarine-like nearshore waters as nursery grounds for demersal fishes (Blaber et al., 1995; Blaber, 2002), much like the role of estuaries in temperate regions (Able, 2005). To further assess this nursery function, future surveys should include the shallowest (< 6 m depth) waters, and use a trawl with a smaller cod end mesh size (e.g. 20 mm) to assess densities of the early life stages as well. Nevertheless, we can conclude that the current ban on industrial trawl fisheries below 18 m depth in Suriname is a valid management measure to protect commercial fish species, by allowing the young fishes to recruit to the adult stocks.

On the other hand, it seems a bit strange that we rarely caught larger, commercial sized sciaenids in our hauls, although they form a main target group in the coastal Suriname fishery. By using a small-sized shrimp trawl, the present study probably underestimated the abundance of larger, more mobile fishes, which are more efficiently sampled by larger trawls with a higher vertical opening (e.g. Wassenberg et al., 1997) and by gillnets, as used by the artisanal fishing fleet in Suriname. Therefore, our results on the densities of larger-sized fishes should be interpreted with care, as they might not have been sampled adequately by the gear used. Nevertheless, larger fishes might have effectively become scarcer due to an increased fishing pressure and the constant adult removal by coastal gillnet fisheries. Already in 1998 declining catch rates indicated that large demersal fishes were overfished (Charlier, 2000), while the number of fishing licenses has not been reduced since (LVV, 2013).

From 18 m onwards, *i.e.* within the *transition* and (deeper) *coastal assemblage*, industrial trawling for *Xiphopenaeus kroyeri* with fine-meshed demersal shrimp trawls is allowed. This fishery has a considerable bycatch of small-sized fishes (Southall et al., 2011). The artisanal fisheries in river estuaries targeting *X. kroyeri* with fine-meshed fyke nets might produce considerable bycatches of non-target (sciaenid) fishes as well (LVV, 2013). Unfortunately, no detailed information on bycatches is currently available. Therefore, bycatch assessments are urgently needed to gain more insight in the impact of these fisheries on the populations of larger demersal (mainly sciaenid) fishes, being the most important fisheries resource in terms of landings and employment in Suriname (Bhagwandin, 2012).

The two stingrays *Dasyatis guttata* and *Gymnura micrura*, which were commonly noted in our surveys, were much smaller than the reported common landing sizes. Although they are not targeted by any fishery, these species are still commonly caught by the *Xiphopenaeus kroyeri* trawl fisheries, despite the use of net adaptations (Willems et al., 2016). In general, elasmobranch populations are highly vulnerable to fishing mortality (Stevens et al., 2000). Besides affecting the length distribution of the more resilient species, fishing activity might have locally wiped out some critically endangered elasmobranchs, such as daggernose shark *Isogomphodon oxyrhynchus* and

sawfishes *Pristis pristis and P. pectinata* (IUCN, 2015), which were caught off Guyana in the 1960s (Lowe-McConnell, 1962) but not observed in the present study. The impact of coastal fisheries on large sized-individuals of commercial and globally threatened elasmobranch species, which are crucial contributors to healthy fish populations (Birkeland and Dayton, 2005), should be properly assessed.

CONCLUSION

The most important feature of the demersal fish community of the Suriname Shelf was a spatial shift from a coastal to an offshore demersal fish species assemblage around the 30 m isobath, corresponding with an important habitat shift. No clear temporal patterns in species composition and abundance were found. In describing the species composition and structuring environmental factors of each assemblage, this paper provides insight in the ecology and distribution of several target species in the multi-species coastal fisheries of Suriname. The current ban on trawl fisheries in most of the nearshore area seems a valid management measure to ensure the nursery function of the nearshore waters. Still, the interaction between the different fishing fleets operating on the inner Suriname Shelf and their impact on commercial and potentially vulnerable species such as sharks and rays should further be assessed.

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PART II

THE ROLE OF *XIPHOPENAEUS KROYERI* IN THE COASTAL FOOD WEB OF SURINAME

4

TROPHIC ECOLOGY OF ATLANTIC SEABOB SHRIMP *XIPHOPENAEUS KROYERI:* INTERTIDAL BENTHIC MICROALGAE SUPPORT THE SUBTIDAL FOOD WEB OFF SURINAME

Modified from:

Willems,T., De Backer, A., Kerkhove, T., Dakriet, N. N., De Troch, M., Vincx, M., Hostens, K. Trophic ecology of Atlantic seabob shrimp Xiphopenaeus kroyeri*: intertidal benthic microalgae support the subtidal food web off Suriname. Submitted to Estuarine, Coastal and Shelf Science.*

A combination of stomach content analyses and dual stable isotope analyses was used to reveal the trophic ecology of Atlantic seabob shrimp Xiphopenaeus kroyeri *off the coast of Suriname. This coastal penaeid shrimp species has a rather omnivorous diet, feeding opportunistically on both animal prey and primary food sources. The species is a predator of hyperbenthic crustaceans, including copepods, amphipods and the luciferid shrimp* Lucifer faxoni, *which are mainly preyed upon during daytime, when these prey typically reside near the seabed. Benthic microalgae (BM) from intertidal mudflats and offshore sedimentary organic matter (SOM) were important primary food sources. Due to their depleted 13C values, coastal sedimentary and suspended organic matter, and carbon from riverine and mangrove-derived detritus were not incorporated by* X. kroyeri. *An ontogenetic diet shift was observed from postlavae to juveniles and adults. Adult* X. kroyeri *were located higher in the food chain, mainly preying on larger benthic organisms. Intertidal BM were an important food source for all life stages of* X. kroyeri, *contributing up to 64 % to the overall diet based on a Bayesian mixing model. Because* X. kroyeri *is the main epibenthic organism found at high densities in nearshore waters up to 30 m depth, the species plays a crucial role in transferring energy from low trophic level prey and primary food sources up to higher levels in the food chain. Our results indicated that primary production on intertidal mudflats, through BM, forms an important energy source for the subtidal turbid-water food web in muddy tropical coasts. Conservation of intertidal areas and their associated mangrove systems will therefore likely benefit coastal shrimp production and fisheries in tropical ecosystems.*

1 INTRODUCTION

River-influenced muddy shorelines with mangrove systems represent a major biome in the tropics, characterizing more than 75 % of the world's coastline between 25°N and 25°S (Flemming, 2002). The adjacent shelf waters often constitute productive environments related to the input of organic matter and nutrients from various sources (Bouillon and Connolly, 2009). River runoff and litter fall from mangrove forests provide terrestrial detritus (Robertson and Alongi, 1995), while riverine nutrient input invokes a high phytoplankton production in the offshore zone adjacent to the turbid nearshore waters (e.g. Smith and Demaster, 1996). Deposition of riverine sediments can create extensive bare intertidal mudflats (e.g. Augustinus, 2004), allowing for a significant primary production of benthic microalgae (MacIntyre et al., 1996).

Penaeid shrimps (Decapoda: Penaeoidea) are a major component of the benthos occupying soft-bottom habitats of tropical shelves (Longhurst and Pauly, 1987; Alongi, 1989). Their exploitation by industrial and artisanal fisheries worldwide, with an annual catch of ca. 1.3 million tons, provides income and employment for hundreds of thousands of fishers (Banks and Macfadyen, 2011). Penaeid shrimps are also known to play a key role in coastal food webs (e.g. Abarca-Arenas et al., 2007). They are low trophic level consumers, feeding on detritus, plant material and small benthic animals (Dall et al., 1990). On the other side, penaeid shrimps pass energy to the higher trophic levels as they are heavily preyed upon by demersal fishes (e.g. Salini et al., 1994), including commercially important fish species (Manickchand-Heileman et al., 1998).

Atlantic seabob *Xiphopenaeus kroyeri* is a rather small penaeid shrimp, widely distributed in the Western Atlantic, from North Carolina (USA) through the Gulf of Mexico and Caribbean Sea to Southern Brazil (Holthuis, 1980). Adult *X. kroyeri* populations live in estuarine and shallow nearshore waters, characterized by fine substrates (Costa et al., 2007; Freire et al., 2011). This in contrast to other penaeid shrimps in the region (mainly *Penaeus sp.*), which are typically found further offshore (Villegas and Dragovich, 1984). *Xiphopenaeus kroyeri* can be very abundant, and locally constitutes the single dominant epifaunal organism up to ca. 30 m depth (e.g. Guéguen, 2000a; Willems et al., 2015b). This makes it an accessible resource for coastal fisheries, being one of the main target species for artisanal fisheries in southern Brazil (Branco, 2005; Silva et al., 2013). In recent decades commercial shrimp trawling has shown increasing interest in *X. kroyeri*, as *Penaeus sp*. stocks further offshore have been largely overexploited (e.g. Chin-A-Lin and IJspol, 2000). This caused a considerable increase in global landings of *X. kroyeri* from ca. 11.000 t in 1990 to nearly 50.000 t in 2013, making it one of the top ten most caught penaeid shrimps in the world (Silva et al., 2013; FAO, 2014a).

Given its importance for fisheries, several aspects on the ecology (e.g. Costa et al., 2007; Castilho et al., 2008; Simoes et al., 2010), reproductive biology (e.g. Heckler et al., 2013a; Castilho et al., 2015), population dynamics (e.g. Castro et al., 2005; Heckler et al., 2013b), and population genetics (Gusmao et al., 2006; Gusmao et al., 2013) of *X. kroyeri* have already been studied. However, whereas this shrimp species is known to contribute to the diet of demersal coastal fishes (Camargo and Isaac, 2004), its general importance for higher trophic levels remains unassessed. Moreover, except for three studies that assessed the diet of *X. kroyeri* by means of stomach content analyses (Cortés and Criales, 1990; Tararam et al., 1993; Branco and Junior, 2001), little attention has been given to the trophic interactions between *X. kroyeri* and potential food sources in the environment. The three studies mentioned above show that the trophic spectrum of *X. kroyeri* exists of more than 30 different prey types, mainly benthic crustaceans. Dependent on the study, unidentifiable organic matter occurred in 13 to 100 % of the analysed stomachs, which raises the question on the real primary food sources for *X. kroyeri*.

The currently available information does not allow to clearly understand the trophic ecology, and hence the ecological role of *X. kroyeri* in tropical coastal food webs. Many penaeid shrimps have complex life cycles, undertaking in-offshore migrations and changing habitats and food sources as they grow from postlarvae to adults (Stoner and Zimmerman, 1988). Understanding these ecological interactions is key in an ecosystem approach for fisheries (Cury et al., 2005). An increased knowledge on the species' trophic ecology may help predicting the potential effect of environmental changes on food availability, and on the subsequent recruitment success and yield for shrimp fisheries (e.g. Pinnegar et al., 2000).

The current study aimed to assess the trophic ecology of *X. kroyeri* on the inner continental shelf of Suriname, an area with muddy nearshore deposits and mangrove coasts, and strongly influenced by riverine input. The objectives were to reveal (1) which of the multiple potential food sources in the area are ingested and assimilated by *X. kroyeri,* and (2) whether food sources change or differ between postlarvae, juvenile and adult shrimps. To reveal basic dietary information on what prey are ingested, stomach content analyses were conducted on adult *X. kroyeri*. Stomach content analysis is an easy and straightforward method for diet studies (Baker et al., 2014), and has been successfully applied to penaeid shrimp (Albertoni et al., 2003), including *X. kroyeri* (Branco and Junior, 2001). However, stomach analysis only provides a 'snapshot' of the diet. It does not allow identifying the food sources that are really assimilated in body tissue, nor allows revealing the origin of organic matter in the shrimp stomachs (Lin et al., 2007). Stomach content analyses were therefore complemented with stable isotope analyses (France, 1998). The combined analysis of the carbon (C) and nitrogen (N) stable isotopes (SI) has been successfully used to identify the dynamics of food webs, including the estimation of the trophic position of different ecosystem components and the

identification of carbon sources fuelling coastal food webs (e.g. Peterson, 1999; Boecklen et al., 2011). Moreover, SI analysis allows for the identification of the food sources of postlarvae and juvenile *X. kroyeri*, which are too small for stomach content analysis. In this study, we compared the carbon (C) and nitrogen (N) SI composition of *X. kroyeri* adults, juveniles and postlarvae with the C-N composition of several potential food sources, including primary sources, such as sedimentary organic matter, suspended particulate organic matter, leaf litter and benthic microalgae, and secondary animal prey sources, *i.e.* macrobenthos, hyperbenthos and zooplankton.

2 MATERIALS AND METHODS

2.1 STUDY AREA

The study was conducted on the inner Suriname Shelf (54 – 57 °W, 6 – 7 °N, Fig. 1), situated in the Guianan Ecoregion of the North Brazil Shelf Province (Spalding et al., 2007). The area is characterised by a wide and gently sloping continental shelve and is profoundly influenced by the turbid freshwater discharge from the Amazon River (Heileman, 2008). Amazon water is carried north-west to the Suriname coast by the North Brazil Current and its extension, the Guiana Current (Johns et al., 1998; Hellweger and Gordon, 2002). Amazon-borne sediments with a mud-content (<63 μm) of 95 – 100 % and a total organic carbon content (TOC) of 1 % dominate the inner shelf deposits up to 20 m depth (Eisma et al., 1991; Augustinus, 2004; Willems et al., 2015b). Mud resuspension by tides and currents causes turbid nearshore waters, with total suspended matter concentrations up to 150 $g.m^{-3}$. Beyond the 20 m depth contour, coarser sediments (median grain size >300 μm; TOC <0.5 %) gradually become more dominant and water turbidity decreases (Willems et al., 2015b). The combination of increased irradiance and coastal nutrient input allows for a high offshore primary production between 20 and 50 km from the coast (Cadée, 1975). Most rainfall in Suriname, and peak discharge of both the Amazon and local rivers, occurs between December and July (Amatali, 1993, Hu et al., 2004). Typical values of salinity and surface temperature of the coastal waters measure around 35 and 28°C, respectively (Willems et al., 2015b).

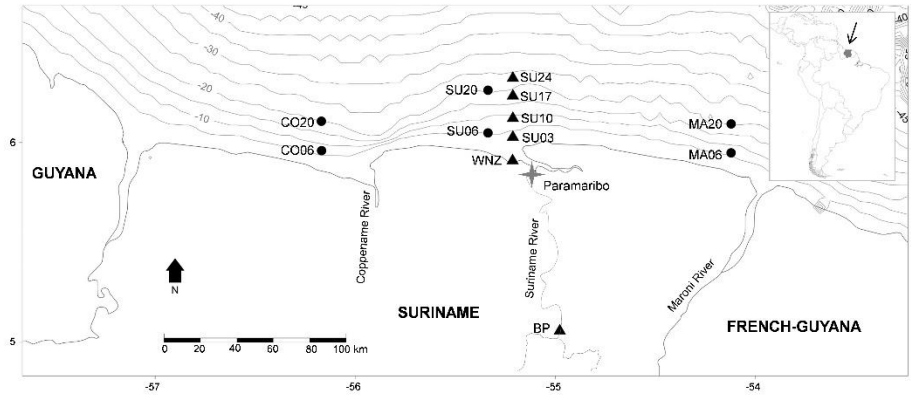

Figure 1. Map of the study area with indication of the sampling locations. Circles indicate 2012-samples, triangles 2014-samples. Numbers in the sample station codes denote approximate water depth. WNZ and BP are land based locations sampled for potential intertidal and terrestrial food sources.

2.2 SAMPLE COLLECTION

Xiphopenaeus kroyeri (both for stomach content and SI analyses) and potential food sources (for SI analyses) were sampled on three different campaigns on board FV *Neptune 6*. Adult *X. kroyeri* and three potential food sources were collected on two surveys in April and July 2012, at six locations across the inner Suriname Shelf (6 and 20 m depth, three transects near the outflow of the Coppename, Suriname and Maroni River) (see Willems et al., 2015b) (Fig. 1). Additionally, a full depth gradient was sampled in February 2014 near the outflow of the Suriname River (SU03, 10, 17 and 24), to collect different *X. kroyeri* life stages (adults, juveniles and postlarvae), and the other potential food sources. As well in February 2014, two land based locations (WNZ and BP) were sampled for potential intertidal and terrestrial food sources (Fig. 1). Table 1 gives an overview of the different samples taken at each location.

Xiphopenaeus kroyeri adults (both for stomach content and SI analyses) were sampled using a small demersal shrimp otter trawl (2.6 m door spread; 45 mm codend mesh size). Individuals were considered adult when the petasma was fused (males) (Fransozo et al., 2011) or when the carapace length (including rostrum) exceeded 33 mm (females) (de Campos B.R. et al., 2009). Individuals for stomach content analyses were preserved in a buffered 4 % formaldehyde solution on board, while samples for SI analyses were immediately frozen (-20 °C).

A hyperbenthic sledge (1 mm mesh size) was used to sample juvenile and postlarval stages of *X. kroyeri,* and to collect potential hyperbenthic food sources (both for SI analysis). The entire hyperbenthic sample was immediately stored frozen (-20 °C) on board until further processing.

Other potential food sources that were collected for SI analysis on the different surveys included (Table 1; Fig 1):

- Macrobenthos; sampled with a Van Veen grab (0.1m²), and obtained by on board sieving of the sediment on a 1 mm mesh sieve;

- Zooplankton; collected by towing a bongo net (200 μm mesh size) in the upper water column;

- Leaf litter; picked out (2-5 leaves) from the trawl catches when present, and further collected from intertidal mud flats at location WNZ;

- Sedimentary Organic Matter (SOM); sampled by scraping off the top 5 mm of seabed sediment samples collected with a Van Veen grab;

- Suspended Particulate Organic Matter (sPOM); seawater sampled at 5 m water depth with a Niskin-bottle; sPOM obtained by filtering 0.3 to 1 l of seawater onto Whatman GF/F glass-fiber filters;

- Riverine sPOM; river water collected upstream the Suriname River at location BP; riverine sPOM similarly obtained by filtering river water onto Whatman GF/F glass-fiber filters;

- Benthic microalgae (BM); sampled on a coastal mudflat at location WNZ following an adapted method proposed by Couch (1989) by scraping off the top layer of intertidal mud in the field and spreading this out in plastic trays for transportation to the lab.

All potential food sources (except for BM) were immediately frozen at -20 °C upon collection, which is a widely accepted preservation method (Bosley and Wainright, 1999; Kaehler and Pakhomov, 2001; Barrow et al., 2008).

Table 1. Overview of sample collection for SI analysis. XK = *Xiphopenaeus kroyeri* (AD = adult; JV = juvenile; PL = postlarva), SOM = sedimentary organic matter, sPOM = suspended particulate organic matter, LL = leaf litter; MB = macrobenthos, HB = hyperbenthos, ZP = zooplankton, BM = benthic microalgae.

Area	Station	Coordinates		Description	April 2012	July 2012	February 2014
		°N	°W				
Brokopondo	BP	5.06	54.98	riverine			sPOM
Weg naar Zee	WNZ	5.91	55.21	intertidal			LL, BM
Marowijne estuary	MA06	5.95	54.12	coastal	XK-AD, SOM, sPOM, LL	XK-AD**, sPOM, LL	
	MA20	6.15	54.12	coastal	XK-AD, SOM, sPOM, LL	XK-AD**, sPOM, LL	
Coppename estuary	CO06	5.96	56.17	coastal	XK-AD, SOM, sPOM, LL	XK-AD**, sPOM, LL	
	CO20	6.06	56.17	coastal	XK-AD, SOM, sPOM, LL	XK-AD**, sPOM, LL	
Suriname estuary	SU06	6.13	55.34	coastal	XK-AD, SOM, sPOM, LL	XK-AD**, sPOM, LL	
	SU20	6.26	55.34	coastal	XK-AD, SOM, sPOM, LL	XK-AD**, sPOM, LL	
	SU03	6.03	55.21	coastal			XK-AD, SOM, sPOM, MB, HB, ZP
	SU10	6.16	55.21	coastal			XK-AD, MB, HB, ZP
	SU17	6.23	55.21	coastal			XK-AD**, XK-JV, XK-PL, MB, HB, ZP
	SU24	6.30	55.21	offshore*			XK-AD**, SOM, sPOM, MB, HB, ZP

*offshore abiotic conditions dominate from >20 m depth onwards (Willems et al., 2015b); **samples for both SI analysis and stomach analysis

2.3 LAB ANALYSES

2.3.1 STOMACH CONTENT ANALYSIS

Stomach content analyses were conducted on 120 adult *X. kroyeri* by randomly selecting 10 individuals from the six July 2012 hauls and 30 individuals from two February 2014 hauls (SU03 and SU10 yielded too few individuals). Carapace length was measured with a calliper to the nearest mm before the stomach was removed by a latero-dorsal cut in the carapace. Stomach content was suspended in a Petri dish with distilled water and all food items in the stomach were identified using a binocular microscope to the lowest taxonomic level possible. The 'points method' was used to assign a relative volumetric contribution (%) to each prey type in the stomachs (Hynes, 1950; Hyslop, 1980; Williams, 1981).

2.3.2 STABLE ISOTOPE ANALYSIS

SI analyses were performed on the different life stages of *X. kroyeri* and the sampled potential food sources. The frozen samples of adult *X. kroyeri*, as well as the hyperbenthos, macrobenthos and zooplankton samples, were thawed

and subsequently sorted using a binocular microscope (within 2 h to avoid label leakage; e.g Moens et al., 1999). Postlarvae of *X. kroyeri* were identified from the hyperbenthos samples using the keys by Cook (1964) and Lins-Oliveira and Lhomme (1993). Individuals of *X. kroyeri* >25 mm total length, but still lacking adult characteristics were considered juvenile (Cook, 1964). Juvenile and postlarval *X. kroyeri* were only encountered in sufficient densities in the SU17-sample.

Potential food sources for *X. kroyeri* from the hyperbenthos samples included amphipods, copepods, chaetognaths, fish larvae, brachyuran zoeae, *Acetes sp.* and *Lucifer faxoni* (the latter discriminated as they were highly abundant species). Potential macrobenthos food sources were sorted to the taxonomic level of sipunculids, polychaetes, bivalves, amphipods and brachyurans. From the zooplankton samples only copepods were retained as potential food source. Only the samples in which a certain taxonomic group (or food source) was found to be highly abundant were selected for further processing.

After sorting, bivalve shells and exoskeletons of *X. kroyeri* and *Acetes sp.* were removed to obtain carbonate-free muscle tissue (Mateo et al., 2008). Next, all samples were rinsed with Milli-Q water and dried for 24 h at 60 °C. Peeling was not feasible for smaller taxa. Therefore, the presence of carbonates was assessed with the 'champagne test' (Jaschinski et al., 2008): brachyurans and brachyuran zoeae were acidified by adding diluted HCl (4 %) to the dried sample until bubbling ceased. For adult *X. kroyeri*, tissue of three individuals was used per sample, while for smaller organisms up to 50 individuals (from a single sample) were pooled to obtain enough material for SI analysis.

Leaf litter and SOM samples, and sPOM filters were thawed, rinsed with Milli-Q water and dried for 24 h at 60 °C. Inorganic carbon was removed from the SOM and leaf litter samples by adding diluted HCl (4 %) to the dried sample until bubbling ceased (Carabel et al., 2006; Fernandes and Krull, 2008). sPOM filters were treated with HCl fumes (40 %) for 5 hours (Lorrain et al., 2003).

The trays with intertidal surface sediment were covered with a thin layer of *in situ* collected seawater and illuminated to allow the migration of benthic microalgae (BM) onto microscopic slides that were placed on top of the sediment with a lens tissue underneath the slide to avoid contamination with sediment. After 24 hours, the slides were removed and washed with filtered seawater, which was then filtered onto Whatman GF/F filters to retain BM. The filters were subsequently rinsed with Milli-Q water and dried for 24 h at 60 °C (Couch, 1989).

All dry samples were grounded (except for GF/F filters) with mortar and pestle to homogeneous powder. From each sample, three aliquots (1.5 mg animal tissue, 3.8 mg leaf litter, 60 mg SOM, whole filters for sPOM and BM) were placed into tin (or silver in case of acidified samples) capsules (8x5 mm;

Elemental Microanalysis). For the 2012 sPOM samples only single replicate GF/F filters were available. Multiwell plates containing all capsules were shipped to UC Davis Stable Isotope Facility (USA) for dual SI analyses (C, N) by means of a continuous flow isotope ratio mass spectrometer (Europa Integra). SI ratios are expressed as δ values where $\delta X = (R_{sample}/R_{standard} - 1) \times 1000$ with X = ^{13}C or ^{15}N and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard reference materials for C and N measurements are carbon in the Vienna Pee Dee Belemnite and atmospheric nitrogen (Peterson & Fry 1987), respectively.

2.4 DATA ANALYSES

2.4.1 STOMACH CONTENT DATA

From the stomach content analyses, the dietary composition for adult *X. kroyeri* was assessed by calculating frequency of occurrence (%FO) and volumetric abundance (%V) indices for all food items found in the stomachs (Hyslop, 1980):

$$\%FO_i = (N_i/N) \times 100$$

$$\%V = (\Sigma S_i/\Sigma S_a) \times 100$$

with N_i the number of stomachs containing prey type *i* and N the total number of non-empty stomachs, S_i the relative volumetric contribution of prey type *i* to the stomach content, and ΣS_a the total volumetric stomach content of all stomachs together (Amundsen et al., 1996).

Data on the proportional prey composition in each stomach were square-root transformed to reduce the influence of abundant prey types before calculating the resemblance matrices based on Bray – Curtis similarity index. The 2012-data (Table 1) were used to test for spatial differences in the adult diet with a one-way PERMANOVA (Permutational ANOVA; Anderson et al., 2008) for the factor 'area' (Coppename *vs.* Suriname *vs.* Maroni area; 20 stomachs for each area), with 'depth' as a random factor. Temporal differences in the adult diet were based on the 'Suriname area' data (Table 1) and tested with a one-way Permanova for the factor 'sampling date' (July 2012 (20 stomachs) *vs.* February 2014 (60 stomachs)). In case of significant effects, the contribution of the different prey types was investigated with one-way SIMPER analyses for the respective factors.

2.4.2 STABLE ISOTOPE DATA

Average (± SD) SI composition of the different *X. kroyeri* life stages and the potential food sources were visualized by means of C-N biplots.

To test for spatial and temporal differences in the C and N SI composition of adult *X. kroyeri,* Euclidean distance similarity matrices were calculated from the $\delta^{13}C$ and $\delta^{15}N$ adult datasets. Spatial differences in C and N SI composition of adult *X. kroyeri* were tested on the 2012-data, using one-way PERMANOVA for the factor 'area' (CO *vs.* SU *vs.* MA area; n = 12 per area), with 'depth' as a random factor. Temporal differences in adult C and N SI composition were based on the 'Suriname area' data, using one-way PERMANOVA for the factor 'sampling date' (April 2012 (n = 6) *vs.* July 2012 (n = 6) *vs.* February 2014 (n = 12)).

To test for differences in C and N SI composition between the different life stages of *X. kroyeri,* Euclidean distance similarity matrices were calculated from the bivariate $\delta^{13}C$ and $\delta^{15}N$ datasets for all processed *X. kroyeri*. One-way PERMANOVA tests were performed using the factor 'life stage' (adult (n = 48) *vs*. juvenile (n = 5) *vs.* postlarvae (n = 6)). In each PERMANOVA analysis, the main test was followed by pairwise tests in case of signicant effects.

Bayesian stable isotope mixing models (Parnell et al., 2010) were further applied to estimate the likely contribution of each food source to the diet of *X. kroyeri* adults, juveniles and postlarvae, using SIAR v4 (stable isotope analysis in R). As input in the models, only a limited number of the potential food sources were used. A first selection criterion was based on the fact that the carbon isotope signal of a consumer closely resembles its food sources (Kohn, 1999), with only a small fractionation per trophic level (Post, 2002). Therefore, the potential food sources that deviated too much in $\delta^{13}C$ values from *X. kroyeri*, were omitted from the models as they obviously did not support any life stage of *X. kroyeri*. Secondly, functionally similar food sources with overlapping isotopic compositions were grouped (Phillips et al., 2005). As such, all animal food sources (*i.e.* the hyperbenthos, macrobenthos and zooplankton taxa) were analysed with a group-averaging hierarchical cluster analysis with SIMPROF tests (significance level 5 %), based on the Euclidean distance resemblance matrix of their $\delta^{13}C$ and $\delta^{15}N$ values. Finally, correlations between the retained food sources were tested prior to running the models, as SIAR cannot differentiate between correlated (Pearson's r > 0.8) sources (Parnell et al., 2010; Carreon-Palau et al., 2013). Concentration dependence was incorporated in the SIAR models to account for differences in C-N ratios among food sources (Phillips and Koch, 2002). Mean (± SD) trophic enrichment factors of 0.4 ± 1.3 for $\delta^{13}C$ and 3.4 ± 1 for $\delta^{15}N$ were used (Post, 2002).

All data analyses were performed in R v.3.0.1 (R Core Team, 2013) and in PRIMER v.6.1.13 with PERMANOVA add-on software (Clarke and Gorley, 2006; Anderson et al., 2008). A significance level of p = 0.05 was used in all tests. PERMANOVA-tests were conducted with unrestricted permutation of raw data in case of single-factor designs, and Monte Carlo corrections were applied when too few (<100) permutations could be calculated (Anderson and Robinson, 2003). In most cases, values are given as averages together with their standard deviation (SD), while contribution estimates in the mixed models are given as 95 % credibility intervals.

3 RESULTS

3.1 STOMACH ANALYSES

Carapace length of the analysed shrimp was on average 20.3 ± SD 3.0 mm, and ranged from 11 to 27 mm. Of the 120 analysed stomachs, three were empty. A total of 25 prey types were identified (Table 2). More than 50 % of the prey types were relatively rare (%FO <10 %). The most recurring prey types were organic detritus, sediment, copepods and unidentified crustaceans. Organic detritus accounted for ca. 50 % of the diet in terms of volume, followed by Crustacea (sum ffi 30 %), plant material and sediment (6 and 7 %, respectively) (Fig. 2).

Dietary composition of *X. kroyeri* did not differ significantly among the three sampled areas (Pseudo-F=2.9; p=0.14). On the other hand, a significant temporal effect was observed (Pseudo-F=14.0; p=0.0001), with an increased contribution of plant material and sediment in the 2012 samples, while Crustacea were more important in the 2014 samples (Fig.2).

Table 2. Frequency of occurrence (%FO) and volumetric contribution (%V) of the prey types in the diet of *Xiphopenaeus kroyeri*, based on 120 adult stomachs.

Prey type	%FO	%V
Organic detritus	100	48.6
Crustacea		
Unidentified sp.	63.3	12.5
Copepoda sp.	76.1	9.4
Amphipoda sp.	27.4	3.9
Lucifer faxoni	24.8	2.7
Ostracoda sp.	19.7	1.0
Acetes sp.	1.7	0.1
Cladocera sp.	1.7	0.1
Mysida sp./mysis larva	1.7	0.1
Xiphopenaeus kroyeri postlarva	0.9	0.03
Brachyura sp. zoea larva	0.9	0.03
Sediment	83.8	7.4
Plant material	36.8	5.9
Sponge spicules	51.3	2.8
Diatomea sp.	29.1	1.4
Polychaeta sp.	17.1	1.2
Plastic fibres	12.8	0.7
Bryozoa sp.	4.3	0.6
Foraminifera sp.	9.4	0.5
Rotifera sp.	5.1	0.3
Radiolaria sp.	6.0	0.3
Insecta sp.	2.6	0.3
Bivalvia sp.	5.1	0.2
Pisces sp. Larva	1.7	0.1
Hydrozoa sp.	2.6	0.1

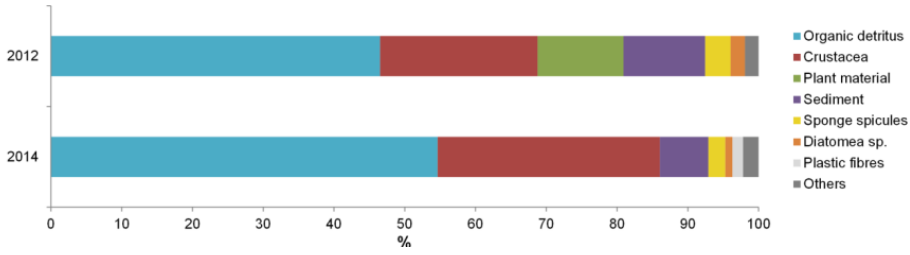

Figure 2. Volumetric contribution (%V) of each prey type in stomachs of *Xiphopenaeus kroyeri* from the 'Suriname area' in 2012 and 2014. All crustaceans grouped and prey types with low contribution (<1 %) lumped as 'Others'.

3.2 STABLE ISOTOPE ANALYSES

3.2.1 SI COMPOSITION OF *XIPHOPENAEUS KROYERI*

No spatial differences among areas were observed in neither $\delta^{13}C$ nor $\delta^{15}N$ of adult *X. kroyeri* (Pseudo-F=1.9; p=0.15 and Pseudo-F=3.0; p=0.06, respectively). $\delta^{13}C$ did not differ between sampling dates either (Pseudo-F=1.2; p=0.33), but $\delta^{15}N$ did (Pseudo-F=14.5; p=0.0001). Whereas adult *X. kroyeri* did not differ in $\delta^{15}N$ between the two 2012-surveys, both had a significantly higher $\delta^{15}N$ (avg. 11.2 ± 0.4 ‰) compared to the 2014-survey (avg. 10.3 ± 0.4 ‰) (pairwise tests, $p < 0.01$).

Both $\delta^{13}C$ and $\delta^{15}N$ differed significantly among *X. kroyeri* life stages (Pseudo-F=54.3; p=0.0001 and Pseudo-F=44.4; p=0.0001, respectively). All lifestages differed significantly in $\delta^{13}C$. $\delta^{15}N$ values of adult *X. kroyeri* were significantly higher than both postlarvae and juveniles, but the latter two did not differ in $\delta^{15}N$ (pairwise tests, $p < 0.01$) (Table 3; Fig.3).

3.2.2 SI COMPOSITION OF THE POTENTIAL FOOD SOURCES

The C-N SI composition of 21 potential food sources, including 8 primary sources and 13 animal prey taxa were identified (Table 3). Riverine sPOM and intertidal and coastal leaf litter showed low $\delta^{13}C$ values below -27 ‰, while coastal sPOM, offshore sPOM and coastal SOM had overlapping $\delta^{13}C$ values between -20 and -25 ‰. The primary sources that were less depleted in ^{13}C were BM (-16.2 ‰) and offshore SOM (-12 ‰) (Table 3; Fig. 3).

$\delta^{13}C$ values of hyperbenthos, macrobenthos and zooplankton prey taxa ranged from -20 to -16.3 ‰ (Table 3; Fig. 3). Cluster analysis distinguished two main groups with overlapping isotope signals, further classified as 'prey group 1' (hyperbenthic and planktonic copepods, bivalves, brachyurans, brachyuran zoeae, *Lucifer faxoni* and macrobenthic amphipods) and 'prey group 2' (hyperbenthic amphipods, sipunculids, fish larvae, chaetognaths, *Acetes sp.* and polychaetes) (Fig.4).

Table 3. Average (± SD) carbon and nitrogen SI composition and C-N ratios for different life stages of *Xiphopenaeus kroyeri* and their potential food sources.

Group/species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C-N	n
Xiphopenaeus kroyeri				
Adult	-14.7 ± 0.2	10.8 ± 0.5	3.2 ± 0.0	48
Juvenile	-15.0 ± 0.2	9.5 ± 0.1	3.3 ± 0.1	5
Postlarvae	-15.7 ± 0.2	9.3 ± 0.2	3.5 ± 0.0	6
SOM				
coastal	-23.0 ± 1.2	6.2 ± 0.8	5.9 ± 0.7	21
offshore	-12.0 ± 0.2	5.4 ± 0.0	10.2 ± 0.2	3
sPOM				
riverine	-33.1 ± 0.2	3.8 ± 0.2	8.5 ± 0.1	3
coastal	-22.6 ± 1.4	5.2 ± 2.2	4.2 ± 1.5	15
offshore	-22.7 ± 0.0	2.9 ± 0.8	5.2 ± 0.2	3
Leaf litter				
intertidal	-27.0 ± 0.1	3.3 ± 0.0	27.6 ± 0.5	3
coastal	-29.2 ± 1.9	6.5 ± 2.4	26.8 ± 11.2	24
Benthic microalgae				
intertidal	-16.2 ± 0.1	6.5 ± 0.1	7.6 ± 0.2	3
Prey group 1				
hyperbenthos				
Copepods	-19.0 ± 0.6	7.1 ± 0.4	4.5 ± 0.1	3
Lucifer faxoni	-20.0 ± 0.6	5.8 ± 0.1	7.4 ± 0.7	3
Brachyuran zoeae	-18.0 ± 0.9	5.2 ± 1.2	5.5 ± 0.5	3
macrobenthos				
Amphipods	-17.7 ± 0.3	6.8 ± 0.1	7.6 ± 0.4	2
Bivalves	-18.2 ± 0.6	7.7 ± 0.4	4.6 ± 0.2	3
Brachyurans	-17.4 ± 0.2	7.0 ± 0.2	5.1 ± 0.2	3
zooplankton				
Copepods	-18.3 ± 0.4	6.6 ± 0.6	4.5 ± 0.2	3
Prey group 2				
hyperbenthos				
Amphipods	-17.2 ± 0.5	8.2 ± 0.7	6.4 ± 0.5	3
Acetes sp.	-16.3 ± 0.0	9.3 ± 0.0	3.8 ± 0.0	3
Chaetognaths	-16.9 ± 0.1	9.1 ± 0.1	4.4 ± 0.0	3
Fish larvae	-17.2 ± 0.3	9.7 ± 0.2	3.8 ± 0.1	3
macrobenthos				
Polychaetes	-17.4 ± 0.1	9.9 ± 0.0	4.6 ± 0.1	3
Sipunculids	-16.7 ± 1.3	8.7 ± 0.6	3.6 ± 0.2	3

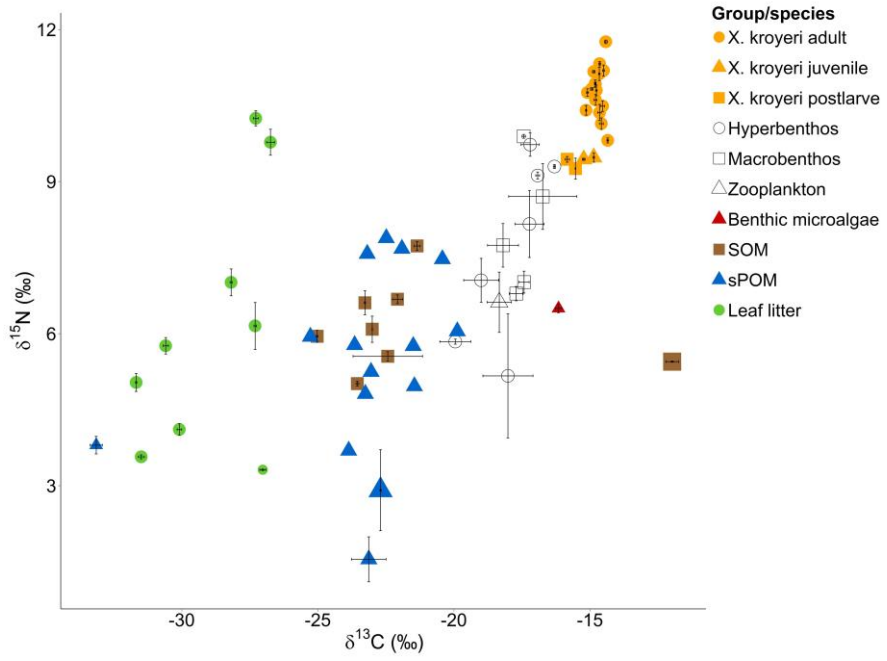

Figure 3. C-N biplot representing average (± SD) values of carbon and nitrogen stable isotopes for different life stages of *Xiphopenaeus kroyeri* and their potential food sources. For the primary food sources, symbols of riverine/intertidal samples are plotted slightly smaller and offshore samples somewhat larger.

3.2.3 SIAR MIXING MODELS

Except for BM and offshore SOM, the other primary sources were not considered to be food sources for any life stage of *X. kroyeri* (all $\delta^{13}C$ > -15.7 ‰) because of their depleted $\delta^{13}C$ values below -20 ‰. As such, only four food sources were retained for the SIAR models: BM, offshore SOM, and prey groups 1 and 2 (Fig. 5). None of these were significantly correlated (Pearsons r < 0.8).

SI mixing models (Fig. 6) showed a rather similar diet for *X. kroyeri* postlarvae and juveniles, characterized by a contribution of BM between 4 – 64 % (95 % credibility interval), while prey group 1 and prey group 2 contributed 1 – 53 %, and the contribution of offshore SOM ranged from 7 to 19 %. The diet of adult *X. kroyeri* was characterized by high contributions of prey group 2 (28 - 50 %) and BM (23 – 49 %), followed by offshore SOM (18 - 20 %), and prey group 1 (0 – 15 %) (Fig. 6).

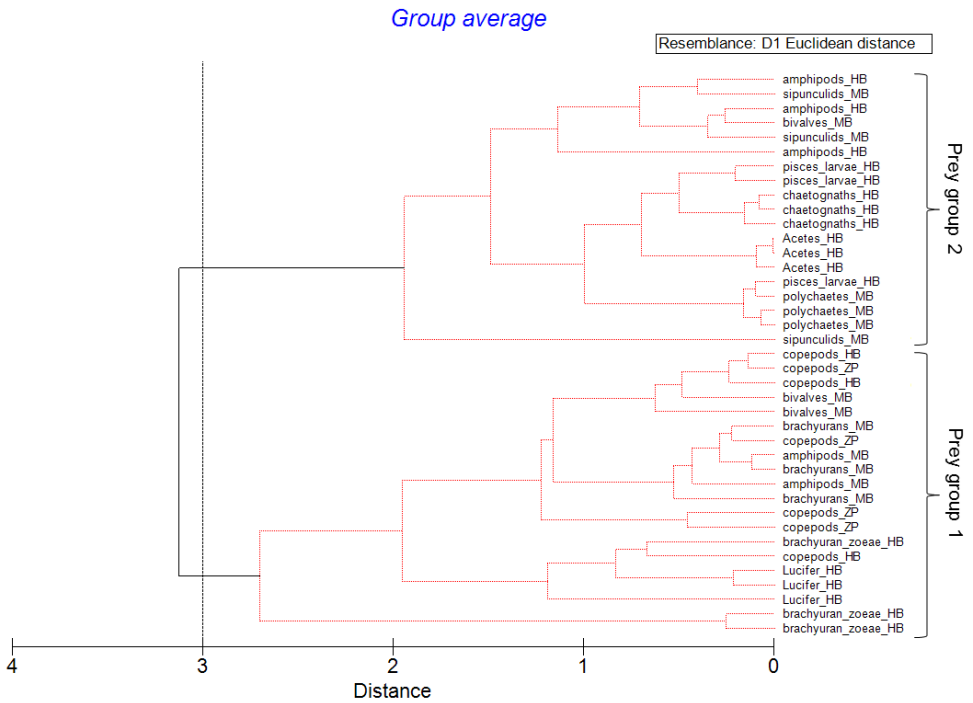

Figure 4. Group-averaging cluster analysis of the Euclidean distance resemblance matrix based on the carbon and nitrogen stable isotope composition of macrobenthos (MB), hyperbenthos (HB) and zooplankton (ZP) food sources. Significant clusters (SIMPROF test 5 % significance level) are indicated by the coloured (red) lines.

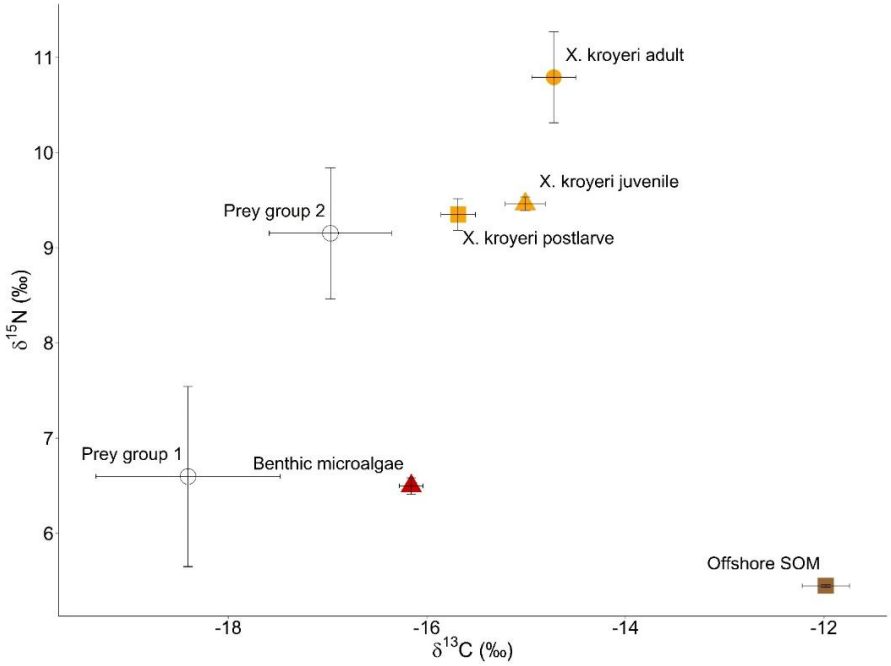

Figure 5. C-N biplot representing average (± SD) values of carbon and nitrogen stable isotopes for different life stages of *Xiphopenaeus kroyeri* and the potential food sources retained in the SI mixing models.

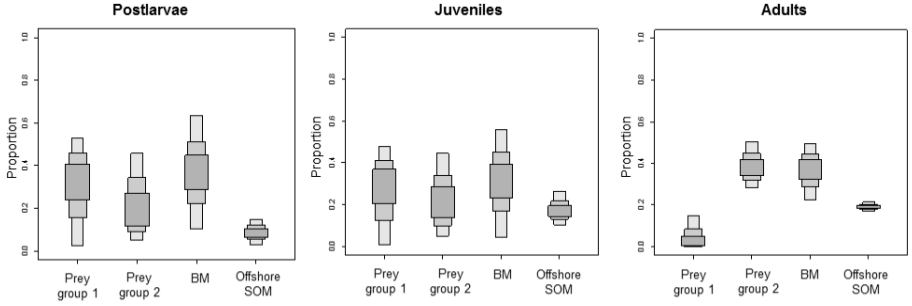

Figure 6. Modelled contribution of the potential food sources to the diet of postlarvae, juvenile and adult *Xiphopenaeus kroyeri*, based on the SIAR stable isotope mixing models. Boxes in different gray shading denote 95 % (light), 75 % and 50 % (darker) credibility intervals.

4 DISCUSSION

4.1 TROPHIC ECOLOGY OF *XIPHOPENAEUS KROYERI*

The stomach content and stable isotope analyses pointed out that *X. kroyeri* has an omnivorous diet, feeding on both small benthic animals and primary food sources. Little spatio-temporal variation was observed in the diet of *X. kroyeri,* but an ontogenetic shift was apparent.

4.1.1 SPATIO-TEMPORAL PATTERNS IN THE DIET OF *XIPHOPENAEUS KROYERI*

Both stomach content analyses and the C-N SI composition indicated that adult *X. kroyeri* had a consistent diet across the study area, with no significant spatial differences. Willems et al. (2015b) showed that the inner Suriname Shelf <20 m depth is characterized by a uniform, muddy seabed habitat with a single coastal epibenthic community. This suggests that probably little spatial variation will be present in the available food sources as well. On the other hand, some slight temporal patterns were observed. The 2012 stomachs contained relatively more plant material than the 2014 samples, possibly related to the higher availability of terrestrial plant material at the end of the long rainy season in July 2012 (Amatali, 1993). This suggests an opportunistic ingestion of food sources, which are readily available in the environment, as has been found for other penaeid shrimps as well (e.g. Nunes et al., 1997). The opportunistic feeding behaviour might also be the reason for the somewhat higher $\delta^{15}N$ signals of the 2012 versus 2014 SI composition of adult *X. kroyeri*. This difference, however, could also be caused by a general upward shift in $\delta^{15}N$ of (part of) the food web due to a temporal shift in primary producer $\delta^{15}N$. The lack of clear spatio-temporal patterns in the SI composition of adult *X. kroyeri* was supported by the stomach content analyses. This justifies the lumping of the SI composition data in the SIAR mixing models, independent of the spatial and temporal spread of the data.

In these mixing models, the widely-used trophic fractionation factors calculated by Post (2002) were used. Trophic fractionation is known to depend on a number of factors, including taxonomic group, the type of tissue and the SI composition value itself, with most variation occurring in the N-isotope (e.g. Vanderklift and Ponsard, 2003; Caut et al., 2009). Nevertheless, when rerunning the SIAR mixing models with two alternative scenarios for $\delta^{15}N$ fractionation (i.e. 2.4 ± 1 and 4.4 ± 1), the estimated contributions of the different food sources to *X. kroyeri* postlarvae, juveniles and adults were almost identical to the original model (with $\delta^{15}N$ fractionation of 3.4 ± 1).

ONTOGENETIC DIET SHIFT

Postlarvae, juveniles and adults of *X. kroyeri* had a different SI composition, indicating an ontogenetic shift in the diet. Postlarvae and juveniles ($\delta^{15}N$ = 9.3 and 9.5 ‰) were situated lower in the food chain than adults ($\delta^{15}N$ = 10.8 ‰). Comparing the SI mixing models for the three life stages, a shift was observed towards the adult stage from lower to higher trophic level prey organisms, as judged from the $\delta^{15}N$ values of the prey (Post, 2002). Prey group 2 organisms ($\delta^{15}N$ ffi 9 ‰) such as chaetognaths, fish larvae and *Acetes sp*. were probably either too large or too mobile to be preyed upon by postlarval and juvenile *X. kroyeri*. Both life stages mainly fed on smaller prey from prey group 1 ($\delta^{15}N$ ffi 6.5 ‰), such as bivalves, copepods and *Lucifer faxoni.* Furthermore, the contribution of offshore SOM was highest in adult *X. kroyeri.* This supports the fact that, like in other penaeid shrimps (Dall et al., 1990), adult *X. kroyeri* live further offshore while younger life stages reside more in very shallow nearshore waters (Oliveira, 1991).

4.1.2 *XIPHOPENAEUS KROYERI* AS OMNIVOROUS FEEDER

Based on the findings of Branco and Junior (2001), *X. kroyeri* has been classified as a secondary consumer, and more specifically as a carnivore animal (Corbisier et al., 2006). The current study is the first to reveal its role as a true primary consumer as well. Therefore, we suggest to classify the species as omnivorous rather than carnivorous, feeding on both benthic animals and primary food sources.

XIPHOPENAEUS KROYERI AS PREDATOR

Both stomach content and SI analyses confirmed the trophic importance of animal prey in the diet of *X. kroyeri*. The fact that penaeid shrimp feed on small fauna is well-known (e.g. Chong and Sasekumar, 1981; Dall et al., 1990). However, penaeid shrimps are typically feeding on infauna (e.g. polychaetes and bivalves), as they search for food by probing the bottom with their pereopods (Dall et al., 1990). Cortés and Criales (1990) also found bivalve and polychaete remains as the dominant prey of adult *X. kroyeri* off Colombia. In contrast, bivalves were rarely found in the stomachs we analysed from Suriname. Polychaetes did occur in 17 % of the adult stomachs, but they do not necessarily belong to the infauna (e.g. Wildish et al., 1992). Generally, infauna is expected to be scarce on the inner Suriname Shelf, due to the instability of the muddy nearshore (<20 m depth) sediments (Aller and Aller, 2004; Willems et al., 2015b).

In our study, SI mixing models estimated >50 % contributions for animal sources (prey group 1 and 2), while crustaceans represented nearly 30 % of the stomach contents of *X. kroyeri* by volume. Tararam et al. (1993) also noted 'unidentified crustaceans' as the main food source for *X. kroyeri*, and Branco

and Junior (2001) identified gammarid amphipods as a main food source (38 % by volume) of adult *X. kroyeri* along the Brazil Coast. Among the crustaceans, we found copepods and the luciferid shrimp *Lucifer faxoni as* important animal food sources, occurring in 76 resp. 25 % of the analysed adult stomachs. Based on the length of the antennas (pers. observation), the majority of the copepods in the stomachs were considered as planktonic (calanoid and cyclopoid) species, while *L. faxoni* is a pelagic species (Teodoro et al., 2012). This raises the question on how and when these organisms were preyed upon, knowing that *X. kroyeri* (like other penaeids) normally reside near the sea bottom. Penn (1984) found that penaeid shrimps from clear waters burrow during the day and only emerge for feeding at night, while such an activity pattern was not seen in turbid waters, where little or no light reaches the bottom. Mauchline et al. (1998) noted that many planktonic copepods reside close to the bottom during the day to avoid predation in the pelagic realm. Similarly, *L. faxoni* is associated with the sea bottom during day time (Woodmansee, 1966; Teodoro et al., 2012). The turbid nearshore waters of the inner Suriname Shelf might allow for *X. kroyeri* to be active around the clock (Freire et al., 2011), feeding preferably during daytime while many of these planktonic animals are associated with the seabed. Overall, our results indicated that *X. kroyeri* may be considered as a predator of hyperbenthic organisms, i.e. animals that live close to the seabed in the lower meter of the water column.

XIPHOPENAEUS KROYERI AS PRIMARY CONSUMER

Unidentified organic detritus occurred in all investigated adult stomachs, representing nearly 50 % of the stomach content by volume. Moreover, based on the SI composition, *X. kroyeri* is situated lower in the food chain than could be expected from previous studies that were based on stomach content analyses alone. Overall, *X. kroyeri* occupies a trophic level between 2 and 3, as assumed by Villeger et al. (2008).

The SI analyses suggested that the primary sources mainly contributing to this unidentified organic detritus were BM and offshore SOM. Judging from their depleted $\delta^{13}C$ values, the other potential primary sources were considered as no real food sources for *X. kroyeri* in the study area. While plant material was encountered in 37 % of the adult stomachs, decomposing leaf litter was most probably only ingested for the nutritional value of its associated bacterial biofilm (Gatune et al., 2012), or by more random feeding. Leaf litter mainly originated from mangroves, which are present all along the Suriname coastline (Latawiec et al., 2014). In contrast to earlier hypotheses (Odum and Heald, 1975), our findings support the theory that mangrove organic matter is only limitedly incorporated into coastal food webs (Lee, 1995; Fry and Ewel, 2003; Chew et al., 2012).

On the other hand, mangrove detritus may be an important contributor to the carbon pool of coastal SOM, which typically exists of a mixture of terrestrial detritus and marine primary production (Bouillon and Boschker, 2006). sPOM in turbid nearshore waters mainly contains suspended sediments (Vantrepotte et al., 2013), hence the depleted $\delta^{13}C$ values similar to coastal SOM (-25 to -20 ‰). In contrast, offshore SOM was more enriched in $\delta^{13}C$ (-12 ‰), making it a potential food source for *X. kroyeri*. It remains unclear which carbon sources caused the enriched signal of this offshore SOM. Most likely, however, the signal results from a high carbonate ($CaCO_3$) content in the offshore sediment, which was not completely removed by acidication with diluted HCl. Although little information is available on the marine sediments off Suriname, the zone beyond the inshore mudbelt is known to harbour fossil coral reefs, causing carbonate-rich sediments (Nota, 1967).

4.2 INTERTIDAL MUDFLATS PROVIDE TROPHIC SUPPORT FOR *XIPHOPENAEUS KROYERI*

BM from intertidal mudflats was the second primary food source that seemed to be directly ingested by *X. kroyeri*. Yokoyama et al. (2009) stated that penaeid shrimps indirectly depend on BM through their intermediate prey, while Newell et al. (1995) also identified BM as a direct food source for penaeid prawns. Based on observations of a golden-brown stained biofilm on the intertidal mudflats in the field (Consalvey et al., 2004) and a microscopic inspection in the lab, we characterized diatoms as the main component of BM in our study. Also, the $\delta^{13}C$ values of BM around -16 ‰ are within the range typically observed for benthic diatoms (e.g. Newell et al., 1995; Yokoyama et al., 2009). The regular encounter of diatoms in the stomachs of adult *X. kroyeri* (FO = 29 %) provides additional support for BM as an important and direct food source, although diatoms may originate from the phytoplankton as well.

BM from intertidal mudflats was estimated to contribute up to 64 % to the diet of juvenile and postlarval *X. kroyeri* in the mixing models. Postlarvae are known to reside in inshore shallow waters (Oliveira, 1991; Torrez, 2015) and might feed directly on BM when intertidal areas are inundated at high tide. Surprisingly, the mixing model for adult *X. kroyeri*, which live down to ca. 30 m depth (Willems et al., 2015b), also estimated a contribution of BM up to 49 % to their diet. Although very little is known on the life cycle and inshore-offshore migrations of *X. kroyeri* in the area, artisanal fisheries for *X. kroyeri* in estuaries suggest that adults periodically reside in inshore areas (Bhagwandin, 2012), where they can feed upon BM from the intertidal mudflats. This signal will be reflected in the SI composition of adult *X. kroyeri* caught more offshore, because the turnover of the SI composition in muscle tissue is low (e.g. Buchheister and Latour, 2010). On the other hand, several authors found that intertidal BM may support offshore production through tidal resuspension and outwelling of BM

(e.g. Herman et al., 2000; Yoshino et al., 2012), which might be an important process on the inner Suriname Shelf as well.

Our study provided evidence for BM as a main carbon and energy source fuelling the coastal food web. The so-called detritus-based food web, typical for the turbid nearshore waters of the Guianan Ecoregion as suggested by Bianchi (1992), may also thrive on BM as important carbon source. We only sampled BM at a single time and location. Because isotopic signatures might vary in space and time, further research should include more extensive sampling of BM along the Suriname coast to confirm the general validity of our results. Further, the relative importance of BM versus *in situ* phytoplankton production (Chew et al., 2012), the significance of imported offshore phytoplankton production, and the trophic importance of bacterial communities associated with decomposing terrestrial and marine detritus (Fry and Ewel, 2003; Gatune et al., 2012), remains to be assessed in order to better understand the carbon flows, and the ecological role of *X. kroyeri* in the food webs off Suriname.

4.3 MANAGEMENT IMPLICATIONS

The current study supports a growing evidence that the BM layer on (bare) intertidal mudflats subsidize secondary production in the subtidal water body (e.g. Underwood and Kromkamp, 1999; Middelburg et al., 2000; Yokoyama and Ishihi, 2007). On the inner Suriname Shelf, *X. kroyeri* seems to play a crucial role in this process. Being the single abundant epibenthic species up to 30 m depth, it acts as a vector for energy from intertidal primary production to subtidal secondary production. Furthermore, the species is known to be a prey for commercially important demersal fishes (Camargo and Isaac, 2004). While the general importance of *X. kroyeri* as a prey for higher trophic levels on the Suriname Shelf is still to be assessed, it can be stated that *X. kroyeri* passes energy from offshore sedimentary organic matter (SOM), intertidal benthic microalgae (BM) and small hyperbenthic prey up the food chain. Fisheries for *X. kroyeri* should therefore be carefully managed, as overexploitation of this key coastal species might lead to trophic cascade effects, with negative consequences at higher trophic levels and the fisheries these higher organisms support.

Intertidal mudflats are an integral part of the dynamic nearshore environment of the tropical muddy coastline (e.g. Augustinus, 2004). Our study showed that primary production on these mudflats is at the basis of the subtidal food chains, in contrast to detritus from the mangrove forests that border them. Nevertheless, mangrove systems provide crucial services such as trapping sediment, reducing erosion and enhancing coastal accretion (Alongi, 2008), which in turn promote the formation of intertidal mudflats. Worldwide, intertidal areas are being lost by land-reclamation (McLusky and Elliott, 2004),

and mangrove forests are being destroyed at a high rate (Blanco et al., 2012). The trophic importance of intertidal mudflats to offshore fisheries production provides an additional argument for the conservation of the tropical muddy coastlines and their associated mangrove systems.

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‘WASP-WAIST’ CONTROL IN A COASTAL BENTHIC ECOSYSTEM? ATLANTIC SEABOB SHRIMP *XIPHOPENAEUS KROYERI* AS A KEY PREY SPECIES FOR THE DEMERSAL FISH COMMUNITY OFF SURINAME

Modified from:

Willems, T., Quilez, I., De Backer, A., De Troch, M., Vincx, M., Hostens, K. 'Wasp-waist' control in a coastal benthic ecosystem: Atlantic seabob shrimp Xiphopenaeus kroyeri *as a key prey species for the demersal fish community off Suriname. Submitted to Marine Ecology Progress Series*

This study assessed the trophic importance of Atlantic seabob shrimp Xiphopenaeus kroyeri *for the demersal fish community on the inner continental shelf of Suriname. The diet of 13 common fish species was investigated by means of stomach content and stable carbon/nitrogen isotope analyses. Atlantic seabob shrimps occurred in the stomachs of 11 fish species, and the isotopic niche of the demersal fish community considerably overlapped with the theoretical isotopic niche of a* X. kroyeri *predator. Two trophic guilds could be discerned: epi-piscivores and benthivores. The first group were mainly Sciaenidae and fed on a mixture of fish and shrimp, with gravimetrical diet contributions of* X. kroyeri *around 40 %. The epi-piscivores also included one fish specialist (*Gymnura micrura*) and two shrimp specialists (*Nebris microps *and* Cynoscion virescens*). The benthivore feeding guild was taxonomically more diverse and showed a more varied diet. Their stomachs contained significant proportions of 'digested debris', partly originating from* X. kroyeri. *The results showed that a significant amount of energy in the benthic food web of the inner Suriname Shelf is channeled at the intermediate trophic level through one single, abundant and productive benthic invertebrate,* X. kroyeri. *This type of 'wasp-waist' trophic control is well-known from pelagic food webs, but this study highlights its potential importance in coastal benthic ecosystems as well. As invertebrates - like Atlantic seabob - are increasingly targeted by marine fisheries, it is crucial to acknowledge their potential role as key prey species, to allow for an ecosystem approach to fisheries management.*

1 INTRODUCTION

Studying the energy flow through the food web is a key issue to understand the structure and functioning of the marine ecosystem (Cury et al., 2005), a prerequisite to apply an Ecosystem Approach to Fisheries (EAF) (Garcia et al., 2003; Pikitch et al., 2004; Garcia and Cochrane, 2005). Two types of control (bottom-up and top-down) are typically proposed to regulate the trophic structure of marine ecosystems (Frank et al., 2007). Bottom-up controlled systems are resource-driven, in which the dynamics of primary producers (e.g. phytoplankton) control the production and biomass of higher trophic levels (e.g. Frederiksen et al., 2006). On the other hand, top-down control is consumer-driven, and implies that predation by high trophic levels controls the abundance and composition of prey at lower trophic levels (e.g. Worm and Myers, 2003). However, a third process has been recognized more recently. 'Wasp-waist' control is a combination of bottom-up and top-down forcing by a small number of abundant, highly productive, and short-lived species at intermediate trophic levels that form a narrow 'waist' through which energy flow in the system is regulated (Rice, 1995; Cury et al., 2000; Hunt and McKinnell, 2006; Fauchald et al., 2011). Typical wasp-waist controlled systems are those of upwelling regions where one trophic level is represented by small pelagic plankton-feeding fish (e.g. sardines and anchovies), dominated by one or at most a few species (Bakun, 2006; Griffiths et al., 2013; Atkinson et al., 2014). With some exceptions (e.g. Manila clam in Venice lagoon; Pranovi et al., 2003), wasp-waist control seems to exist mainly in pelagic ecosystems, with little evidence for this process acting in benthic food webs.

On soft-bottom habitats of tropical shelves, penaeid shrimps (Decapoda: Penaeoidea) are a major component of the benthos (Alongi, 1989; Longhurst and Pauly, 1987). They are fast-growing and short-lived (Dall et al., 1990), and they occupy a mid-trophic level position (e.g. Manickchand-Heileman et al., 1998; Villeger et al., 2008; Willems et al., submitted a). Ecosystem models show that penaeid shrimp are fundamental for the structural cohesion of the trophic network on (sub)tropical shelves (e.g. Abarca-Arenas et al., 2007). Similar to small pelagic fishes in upwelling systems (e.g. the effect of ENSO on Peruvian anchovy stocks; Gutierrez et al., 2007), penaeid shrimp populations are bottom-up regulated by environmental factors. In particular, temporal variations in river discharge have shown to significantly affect penaeid shrimp recruitment, and subsequent yields to fisheries (e.g. Galindo-Bect et al., 2000; Moller et al., 2009). On the other hand, demersal fishes might exhibit top-down control on shrimp populations by heavy predation (e.g. Pauly and Murphy, 1982; Salini et al., 1994; Manickchand-Heileman et al., 1998), highlighting the importance of penaeid shrimps for higher trophic levels.

The penaeid Atlantic seabob shrimp *Xiphopenaeus kroyeri* is widespread in the Western Atlantic (Holthuis, 1980), living in estuarine and shallow nearshore waters characterized by fine substrates (Costa et al., 2007, Freire et al., 2011). In the productive, Amazon influenced shelf waters off Suriname (Heileman, 2008; Anthony et al., 2010), *X. kroyeri* is the only abundant epibenthic species occurring up to 27 m depth (Willems et al., 2015b). Bottom-trawl fisheries operating on the Suriname Shelf annually land some 10,000 tons of seabob shrimp (Southall et al., 2011), which is about a fifth of the global production (FAO, 2014a). Although trophic links with *X. kroyeri* are still poorly understood, the species is known to occupy a mid-trophic level position (Villeger et al., 2008), feeding on a variety of benthic organisms, including benthic microalgae on intertidal mudflats (Cortés and Criales, 1990; Branco and Junior, 2001; Willems et al. submitted a). On the other hand, *X. kroyeri* is preyed upon by demersal fishes (Camargo and Isaac, 2004), and was identified as the potential main food source for the diverse demersal fish community on the inner Suriname Shelf (Willems et al., 2015a). As such, *X. kroyeri* might act as a wasp-waist controlling organism in the coastal benthic ecosystem off Suriname.

The present study evaluates the trophic importance of *X. kroyeri* for higher trophic levels, by assessing the diet of the demersal fish community on the inner Suriname Shelf. Diet of the most abundant demersal fish species was investigated by means of stomach content and stable isotope analyses. Stomach content analysis is an easy and reliable method to study fish diet (Baker et al., 2014), while carbon and nitrogen stable isotope composition reveal information on assimilated carbon sources and trophic level position, respectively (Peterson and Fry, 1987; Fry, 2006; Boecklen et al., 2011). Both techniques are often combined in diet studies, providing complementary information (e.g. Lin et al., 2007; Zamzow et al., 2011; Layman and Allgeier, 2012). Through these analyses, this study further elaborates on the potential wasp-waist control mechanism and on the potential implications for the management of the commercial seabob fishery and the artisanal fishery in the coastal benthic ecosystem off Suriname.

2 MATERIALS AND METHODS

2.1 STUDY AREA

The study was conducted on the inner (<40 m depth) Suriname Shelf (54 – 57 °W, 6 – 7 °N, Fig. 1), part of the Guianan Ecoregion of the North Brazil Shelf Province (Spalding et al., 2007). The area is characterised by a wide and gently sloping continental shelf, and is under profound influence of the turbid freshwater discharge from the Amazon River (Heileman, 2008). Amazon water is carried north-west to the Suriname Shelf by the North Brazil Current and its extension, the Guiana Current (Johns et al., 1998; Hellweger and Gordon, 2002).

Amazon-borne sediments dominate the inner shelf deposits up to 20 m depth (Eisma et al., 1991; Augustinus, 2004; Willems et al., 2015b), and mud resuspension by tides and currents causes turbid nearshore waters. Sediment grain size and water clarity increases beyond the 20 m depth contour. Average values of salinity and surface temperature of the coastal waters measure around 35 and 28°C, respectively (Willems et al., 2015b).

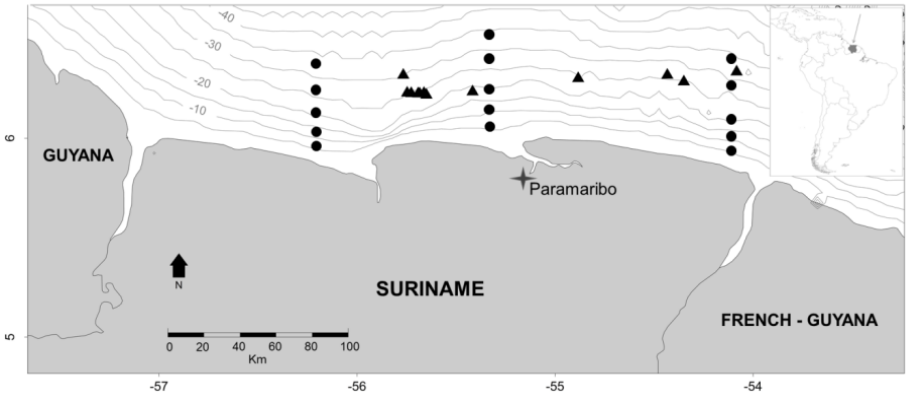

Figure 1. Map of the study area with indication of the sampling locations. Circles ( ) indicate stations sampled for stomach analyses during a demersal trawl survey (2012-2013), triangles (▲) indicate stations sampled during commercial shrimp trawl catches (2014) for both stomach and stable isotope analyses.

2.2 DATA ORIGIN

2.2.1 SAMPLING

Most samples for stomach content analyses were collected during demersal trawl surveys on the inner Suriname Shelf from February 2012 to April 2013, where each time 15 locations were sampled between 6 and 34 m depth (Willems et al., 2015a; Willems et al., 2015b). Additional stomach samples were collected from commercial shrimp trawl catches in April and November 2014. All samples for stable isotope (SI) analyses were taken from the commercial catches in November 2014 (Fig. 1). Sampling was conducted onboard FV Neptune-6, a 25-m long commercial outrigger trawler used in the Suriname seabob shrimp trawling fleet. A small otter trawl at the stern of the vessel was used during the 2012 – 2013 trawl surveys, while the 2014 samples were collected with twin-rig bottom trawls fished from the outriggers. Large fishes were measured onboard to the nearest cm (total length), their digestive tract was cut off at the oesophagus and the anus, and fixed in 8% formaline. Small fishes were injected in the stomach with, and stored entirely in 8% formaline, and measured and dissected in the lab. Fishes for SI analyses were immediately frozen at - 20 °C onboard, which is a widely accepted preservation method

(e.g. Bosley and Wainright, 1999; Kaehler and Pakhomov, 2001; Barrow et al., 2008).

2.2.2 SPECIES AND LENGTH SELECTION

The most common demersal fish species in het study area were selected for diet analysis. These were defined as species occurring in more than 30 % of the 148 bottom trawl samples taken on the inner Suriname Shelf in 2012 and 2013 (see Willems et al., 2015a). In total 13 species were selected, including 11 finfish and two ray species, belonging to seven different families (Table 1). Based on length data from Willems et al. (2015a), the entire length range of the fish species was considered to account for ontogenetic diet shifts. For SI analyses, the length range was divided up to three length classes: small (S), large (L) and extra large (XL), defined as S <25 cm ≤ L <45 cm ≤ XL.

Table 1. Fish species selected for diet analyses, their relative occurrence in the study area, and the investigated length range (total length for finfish; body width for rays). For each species, the total number of investigated stomachs and the investigated length classes for stable isotope (SI) analyses (S < 25 cm ≤ L < 45 cm ≤ XL) are given.

Family Species	Common name	Occurrence* (%)	Length range (cm)	Number of stomachs	Length classes SI analyses
Sciaenidae					
Cynoscion jamaicensis	Jamaica weakfish	68	4 - 21	33	S
Cynoscion virescens	Green weakfish	46	11 - 84	51	S - L - XL
Macrodon ancylodon	King weakfish	57	10 - 37	92	S - L
Nebris microps	Smalleye croaker	45	9 - 37	66	S - L
Paralonchurus brasiliensis	Banded croacker	32	7 - 29	63	S - L
Stellifer microps	Smalleye stardrum	53	9 - 19	39	S
Stellifer rastrifer	Rake stardrum	64	12 - 23	48	S
Achiridae					
Achirus achirus	Drab sole	43	7 - 20	31	S
Cynoglossidae					
Symphurus plagiusa	Duskycheek tonguefish	38	11 - 19	32	S
Dasyatidae					
Dasyatis guttata	Longnoze stingray	71	16 - 67	71	S - L - XL
Gymnuridae					
Gymnura micrura	Smooth butterfly ray	47	15 - 71	65	S - L - XL
Triglidae					
Prionotus punctatus	Bluewing searobin	34	5 - 29	67	S - L
Ariidae					
Amphiarius rugispinis	Softhead sea catfish	62	10 - 34	98	S - L

* % occurrence in 148 demersal trawl samples taken in the study area in 2012 – 2013 (see Willems et al., 2015a)

2.3 LAB ANALYSES

2.3.1 STOMACH CONTENT ANALYSES

At least 30 stomachs were investigated for each fish species (Table 1). Only stomachs (no intestines) were considered. Using a stereomicroscope, prey taxa were identified to the lowest possible taxonomic level and counted. When digestion state permitted, carapace length (excluding the rostrum) of shrimps in the stomachs was measured to the nearest millimetre. Shrimps that could not be identified to a lower taxonomic level were termed 'shrimp-like Decapoda sp.' Unidentifiable items were grouped as 'digested debris' (with abundance = 1 when present in a stomach). Dry weight (DW), and ash weight (AW) of every prey type was measured to the nearest 0.0001 g. DWs were acquired by drying the stomach contents in an oven at 60°C for 48 h. AW was obtained by muffling the DW samples at 550°C for 2 h. When combining these data, the ash-free DW (AFDW = DW - AW) was calculated.

2.3.2 STABLE ISOTOPE (SI) ANALYSES

In the lab, fishes were thawed, and a small piece of muscle tissue from the tail (finfish) or the wing (rays) was cut out and rinsed with Milli-Q water. For each length class muscle tissue of ten fishes of variable length was pooled and dried (48 h at 60 °C). Dry samples were grounded with mortar and pestle into homogeneous powder, and for each sample three 1.5 mg aliquots were placed into tin capsules (8x5mm; Elemental Microanalysis). Multiwell plates containing all capsules were shipped to UC Davis Stable Isotope Facility (USA) for dual SI analysis (C, N) using a continuous flow isotope ratio mass spectrometer (Europa Integra). SI ratios are expressed as δ values where $\delta X = (R_{sample}/R_{standard} - 1) \times 1000$ with X = ^{13}C or ^{15}N and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard reference materials are carbon in the Vienna Pee Dee Belemnite and atmospheric nitrogen (Peterson & Fry 1987) for C and N measurements, respectively.

2.4 DATA ANALYSES

2.4.1 STOMACH CONTENT DATA

DIET INDICES

Thirty-seven empty stomachs were omitted from all analyses. For each non-empty stomach (n=719), the fullness index (FI; Berg, 1979) was calculated as an indicator of feeding activity.

$$FI = \frac{AFDW_s x\ 100}{AFDW_f}$$

$AFDW_s$ represents the summed weight of all prey items in the stomach, and $AFDW_f$ the weight of the entire fish. To obtain $AFDW_f$, fish wet-weight (WW) was calculated from length-weight regressions in the literature, as published on FishBase (Froese and Pauly (Eds.), 2014). Fish WW was then converted to AFDW with the common formula AFDW ffi 0.2 * WW (Edgar and Shaw, 1995; Van Ginderdeuren et al., 2014).

As a measure for fish dietary diversity and niche breadth, prey species richness (S) and Shannon-Wiener diversity index (H') were calculated. Next, the dietary importance of each prey type was assessed using the occurrence (%FO) and abundance (%A) indices (Hyslop, 1980).

$$\%FO_i = \frac{N_i}{N}\ x\ 100$$

$$\%A_i = \frac{\sum S_i}{\sum S_a}\ x\ 100$$

N_i is the number of fishes with prey type i in the stomach, and N the total number of non-empty stomachs. S_i is the stomach content composed by prey type i and S_a the total stomach content (Amundsen et al., 1996). The abundance index A_i can be numeric (%N; based on counts) or gravimetric (%G; based on AFDW).

To further evaluate the dietary importance of each prey type, the feeding coefficient (Q = %N x %G) (Hureau, 1970) was calculated. Q classifies preys as preferential when Q>200, secondary for 20<Q<200 and accidental for Q<20 (Hureau, 1970). In addition, the SURF (SUpportive Role to Fishery ecosystems) index was calculated for each prey type (Plaganyi and Essington, 2014). This index weighs the importance of a prey type in the food web by considering its interactions with predators, relative to the total number of interactions in the food web. The SURF index for a prey type i with S predators is:

$$SURF_i = \frac{\sum_{j=1}^{S} p_{ij}^2}{L}$$

with p_{ij} the diet fraction of predator j on prey type i, and L the total number of predator-prey interactions in the food web. L was calculated as the number of non-zero interactions between all identified prey types and the 13 investigated fish species. SURF values >0.001 are indicative of 'key' prey species; lower values signify less trophic importance for higher trophic levels (Plaganyi and Essington, 2014).

DIET COMPOSITION PER SPECIES

Diet of the different species was assessed based on gravimetrical prey data (AFDW). Biomass data are best suited to evaluate the relative importance of preys within the predators' diet, while numerical data rather represent the influence of predation on preys (Bowen, 1996). Moreover, biomass data better reflect the relative importance of large prey items and items that are difficult to quantify numerically, such as 'digested debris'. Prior to the analyses, prey types were lumped in groups representing higher-level taxa or individual prey types with high contributions, the remaining items were grouped as 'others'. Gravimetrical prey data were converted to relative values (% of diet by weight) for each sample and subsequently arcsine transformed, which is appropriate for percentages and proportions (e.g. Jaworski and Ragnarsson, 2006).

The diet composition of each fish species was first plotted in length classes of 5 cm to reveal whether important ontogenetic diet shifts occurred (Annex 5.1). Despite some small variations, no obvious ontogenetic differences in the dietary contribution of *X. kroyeri* were apparent. Stomach content data were therefore further considered per species, regardless of length.

Dietary similarity among species was assessed using group-average cluster analyses (Clarke and Gorley, 2006) and principal coordinates analyses (PCO; Anderson et al., 2008). Both analyses were based on a resemblance matrix of the distances among centroids for the grouping factor 'species', which were calculated from a resemblance matrix with Bray-Curtis similarities among samples (stomachs). The most important prey types characterizing cluster groups were identified with a one-way SIMPER analysis. Further, average stomach fullness (FI) and prey diversity in (terms of S and H') were compared among cluster groups with one-way PERMANOVA (Permutational ANOVA; Anderson et al., 2008) analyses based on Euclidean distance resemblance matrices. To visualize prey types that correlated with the first two PCO axes, vectors were overlaid on the PCO ordination plot. Only prey types that had a vector length >0.3, based on multiple correlation, were included for visualisation in the PCO plot (Anderson et al., 2008).

2.4.2 SI ANALYSIS

COMPARISON AMONG SPECIES AND LENGTH CLASSES

Differences in the C and N SI composition of the different fish species/length class combinations were tested with two-way PERMANOVA analyses with the factors 'species' and 'length class', based on Euclidean distance resemblance matrices, calculated from the $\delta^{13}C$ and $\delta^{15}N$ datasets of fish SI composition. Pairwise tests were conducted in case of significant effects main effects.

PREDATION ON *XIPHOPENAEUS KROYERI*

Isotopic niches of species or communities are a proxy for trophic ecology (Layman et al., 2007), and were defined by calculating the standard ellipse areas with small sample size correction (SEA_c) (Jackson et al., 2011). Standard ellipses contain about 40 % of the data, and are less sensitive to small sample sizes than convex hulls (Jackson et al., 2011), which use the full extent of the SI data (Layman et al., 2007). Standard ellipses were calculated for each species/length class combination separately, and for all fishes together, representing the demersal fish community isotopic niche.

The extent of overlap between standard ellipses in a two dimensional (δ13C and δ15N) space is a measure for dietary overlap among species or communities (Jackson et al., 2012; Parnell and Jackson, 2013; Guzzo et al., 2013). Consequently, overlap with the isotopic niche of an *X. kroyeri* consumer can be used as a proxy for predation on *X. kroyeri*. The theoretical isotopic niche of a consumer feeding (exclusively) on *X. kroyeri* was calculated by applying isotopic fractionation to the SI composition of *X. kroyeri* (obtained from Willems et al. submitted a). In contrast to earlier assumptions (e.g. Deniro and Epstein, 1981; Peterson and Fry, 1987), isotopic fractionation (i.e. the differences in isotopic composition between an animal and its diet) might vary considerably depending on a number of environmental and physiological factors (Phillips et al., 2014). Important sources of variation include the taxonomic group and type of investigated tissue (e.g. McCutchan et al., 2003; Vanderklift and Ponsard, 2003; Ankjaero et al., 2012), and the isotopic composition of the food source (e.g. Dennis et al., 2010; Hussey et al., 2014). This variability was accounted for by calculating trophic fractionation factors through equations reported in Caut et al. (2009), specifying isotopic fractionation factors for fish muscle tissue as:

$$\Delta\delta^{13}C = -0.248\delta^{13}C - 3.4770$$

$$\Delta\delta^{15}N = -0.281\delta^{15}N + 5.879$$

This resulted in average isotopic fractionations of 0.3 ± 0.1 for $\Delta\delta^{13}C$ and 2.3 ± 0.1 for $\Delta\delta^{15}N$. The calculated $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ values were applied to each data point of *X. kroyeri* SI composition, and the resultant data were used to estimate theoretical SEA_c's of a general *X. kroyeri* consumer (based on all data; n=29), and of consumers of *X. kroyeri* adults (n=18) and juveniles/postlarvae (n=11). The theoretical SEA_c of *X. kroyeri* consumers were then drawn on C-N biplots, and their overlap with fish SEA_c's was evaluated.

Finally, we assessed the trophic importance of *X. kroyeri* relative to other potential prey types for which local SI composition data were available, based on their $\delta^{13}C$ values. $\delta^{13}C$ is generally used to trace food sources (Kohn, 1999; Boecklen et al., 2011), whereas $\delta^{15}N$ mainly provides information on trophic

position (e.g. Post, 2002). This was done by a graphical comparison (box-and-whisker plots) of the $\delta^{13}C$ values of all 13 demersal fish species, *X. kroyeri* (general, adults and juveniles/postlarvae), and other potential animal food sources sampled in the study area earlier (see Willems et al. submitted a). Following the latter study, the potential animal food sources were lumped in two 'prey groups' based on their C-N isotopic composition: 'prey group 1' included hyperbenthic and planktonic copepods, bivalves, brachyurans, brachyuran zoeae larvae, macrobenthic amphipods and the luciferid shrimp *Lucifer faxoni*; 'prey group 2' contained hyperbenthic amphipods, sipunculids, fish larvae, chaetognaths, polychaetes and the sergestid shrimp genus *Acetes sp.*

SI data were analyzed using the SIBER (Stable Isotope Bayesian Ellipses in R) routine in the SIAR package for R v3.1.3 (Parnell et al., 2010; Jackson et al., 2011; Parnell and Jackson, 2013; R Core Team, 2015). Other data analyses were performed in PRIMER v.6.1.13 with Permanova add-on software (Clarke and Gorley, 2006; Anderson et al., 2008). A significance level of p=0.05 was used in all tests, and Monte Carlo corrections were applied when too few (<100) permutations could be calculated (Anderson and Robinson, 2003). In the results, average values are reported with their standard deviation (SD).

3 RESULTS

3.1 STOMACH CONTENT ANALYSIS

3.1.1 GENERAL DIET CHARACTERIZATION

A total of 756 stomachs were analyzed, of which 37 (4.9 %) were empty. Stomach fullness indices ranged from 0 to 25.8, with an average of 0.5 ± 1.7. Seventy-two different prey types were identified from the stomachs (Table 2). Stomachs contained up to 9 different prey types, with an average of 2.4 ± 1.5 per stomach. Prey diversity (H') was on average 0.6 ± 0.5, with a maximum of 2.0.

The majority of the prey types were rare: 59 occurred in <3 % of the samples. Unidentifiable 'digested debris' occurred in 75 % of all stomachs. Only eight other prey types had a relatively high occurrence: unidentified Pisces sp. (%FO = 25 %), shrimp-like Decapoda sp. (18 %), *Xiphopenaeus kroyeri* (12 %), unid. Polychaeta sp. (12 %), unid. Decapoda sp. (9 %), unid. Brachyura sp. (8 %), *Ogyrides sp.* (8 %) and unid. Amphipoda sp. (6 %). The first four of these had relatively high Q values (>20) as well (Table 2). Three prey types had a SURF score >0.001: unid. Pisces sp. (0.008), digested debris (0.008) and *X. kroyeri* (0.003).

Gravimetrically, *X. kroyeri* was the third most important prey type, contributing 11 % to the diet of the demersal fish community by weight. Carapace length of *X. kroyeri* found in the stomachs was on average 10 ± 5.1 mm. When including shrimp like Decapoda sp., the potential gravimetrical contribution of *X. kroyeri* raised to 15 %. Only digested debris (26 %) and Pisces sp. (23 %) had a higher average gravimetrical contribution (Fig. 2). Based on the texture and white color of digested debris in the stomachs, it was assumed it mainly originated from fish or shrimp tissue (K. Hostens, pers. comm.).

Table 2. List of prey types encountered in the stomachs of 13 demersal fish species. The average relative importance of each prey type is indicated with the frequency of occurrence (%FO), numerical (%N) and gravimetric (%G) abundance index and feeding coefficient (Q = %N x %G) (see Annex 5.1 for tables per species).

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	12.1	7.5	4.9	36.9
Aonides sp.	1.3	0.7	0.2	0.1
Cirratulidae sp.	0.4	0.2	0.7	0.2
Platyhelminthes				
Platyhelminthes sp.	4.1	1.6	0.1	0.1
Crustacea				
Unidentified sp.	2.6	2.3	0.8	1.8
Amphipoda				
Unidentified sp.	6.2	3.1	0.3	0.9
Caprellidae sp.	0.1	<0.1	<0.1	<0.1
Copepoda				
Unidentified sp.	0.5	0.1	0.5	0.1
Cumacea				
Unidentified sp.	0.1	<0.1	<0.1	<0.1
Decapoda				
Unidentified sp.	8.9	3.5	1.8	6.4
Mysid-like decapoda sp.	1.6	2.9	0.2	0.5
Shrimp-like decapoda sp.	18.0	7.7	4.1	31.8
Shrimp-like decapoda sp. postlarva	2.7	4.8	0.1	0.5
Acetes americanus	0.7	0.2	0.1	<0.1
Axiidae sp.	1.9	0.5	0.2	0.1
Nephropidae sp.	0.7	0.2	0.3	0.1
Sicyonia sp.	0.4	0.3	0.2	0.1
Solenocera sp.	0.1	<0.1	0.1	<0.1
Anomura				
Unidentified sp.	0.7	0.1	0.1	<0.1
Clibanarius foresti	0.1	<0.1	<0.1	<0.1
Diogenidae sp.	0.1	<0.1	<0.1	<0.1
Porcellanidae sp.	0.2	0.1	0.1	<0.1
Brachyura				
Unidentified sp.	7.6	2.5	2.1	5.3
Unidentified sp. larva	0.1	<0.1	<0.1	<0.1
Calappa sp.	1.2	0.3	0.2	0.1
Calappidae sp.	2.5	2.3	1.2	2.7
Callinectes sp.	0.1	<0.1	0.2	<0.1
Dromiidae sp.	0.1	<0.1	<0.1	<0.1
Hepatus gronovii	0.4	0.1	0.8	0.1
Hepatus pudibundus	0.1	<0.1	0.2	<0.1
Leiolambrus nitidus	0.1	<0.1	<0.1	<0.1
Portunidae sp.	1.2	0.3	0.3	0.1
Portunus gibbesii	0.2	0.1	0.7	<0.1
Portunus sp.	0.2	<0.1	0.2	<0.1
Caridae				
Exhippolysmata oplophoroides	3.5	1.1	1.5	1.7
Nematopalaemon schmitti	2.3	1.1	1.8	2.0
Ogyrides sp.	7.6	6.0	1.6	9.4
Palaemonidae sp.	0.2	0.1	0.1	<0.1
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.3	<0.1	0.4	<0.1
Penaeus sp. postlarva	1.8	0.5	0.1	0.1
Penaeus brasiliensis	0.1	<0.1	<0.1	<0.1
Penaeus subtilis	0.1	<0.1	1.0	0.1
Rimapenaeus similis	0.1	0.1	0.5	<0.1
Rimapenaeus sp.	0.5	0.2	0.5	0.1
Xiphopenaeus kroyeri	12.0	5.6	10.9	61.2
X. kroyeri postlarve	3.8	2.2	0.5	1.0
Mysida				
Unidentified sp.	0.2	0.1	<0.1	<0.1
Stomatopoda				
Unidentified sp.	2.0	0.1	0.2	<0.1
Unidentified sp. larva	0.5	0.2	<0.1	<0.1
Squilla sp.	0.8	0.2	0.4	0.1
Squilla lijdingi	3.0	1.1	3.6	4.0
Squilla obtusa	0.4	0.1	0.2	<0.1
Mollusca				
Bivalvia				
Unidentified sp.	1.9	0.4	0.1	<0.1
Mactridae sp.	0.1	<0.1	<0.1	<0.1
Nuculidae sp.	0.1	0.1	0.2	<0.1
Pectinidae sp.	0.1	<0.1	<0.1	<0.1
Veneridae sp.	0.1	<0.1	<0.1	<0.1
Gastropoda				
Gastropoda sp.	0.3	0.2	0.1	<0.1
Volutomitridae sp.	0.2	<0.1	<0.1	<0.1
Pisces				
Unidentified sp.	24.6	12.7	22.6	286.4
Clupeiformes sp.	0.2	0.1	0.9	0.1
Amphiarius sp.	0.2	0.1	0.1	<0.1
Harengula jaguana	0.2	0.1	0.8	<0.1
Symphurus plagiusa	0.3	0.1	0.6	0.1
Engraulidae				
Anchoviella lepidentostole	0.2	0.1	0.7	0.1
Engraulidae sp.	0.3	0.2	0.2	<0.1
Sciaenidae				
Cynoscion jamaicensis	0.5	0.3	0.6	0.2
Macrodon ancylodon	0.5	0.2	0.7	0.1
Paralonchurus sp.	0.3	0.1	0.6	0.1
Stellifer rastifer	0.6	0.4	2.2	0.9
Others				
Digested debris	74.7	24.8	25.7	637.9
Plastic fibres	0.4	0.1	<0.1	<0.1

3.1.2 DIET COMPOSITION PER SPECIES

Xiphopenaeus kroyeri occurred in the diet of 11 out of the 13 investigated demersal fish species, and was only absent from the diet of *Achirus achirus* and *Gymnura micrura*. The highest dietary contributions of *X. kroyeri* were found for *Nebris microps* (41 – 49 %) and *Cynoscion virescens* (40 – 52 %; excluding and including shrimp-like Decapoda sp., respectively). Other species with important contributions of *X. kroyeri* were *Macrodon ancylodon* (13 – 15 %), *Stellifer rastrifer* (10 – 15 %), *Stellifer microps* (7 – 14 %), *Cynoscion jamaicensis* (4 – 14 %), *Prionotus punctatus* (3 – 13 %) and *Dasyatis guttata* (1 – 13 %) (Fig. 2).

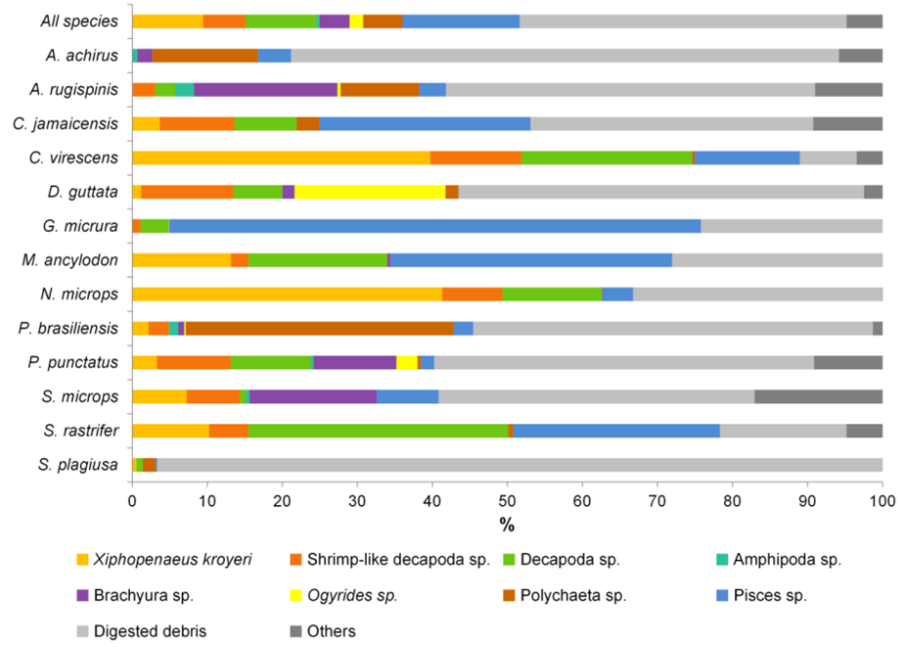

Figure 2. Gravimetrical diet composition of 13 demersal fish species (overall and separate per species). Prey types were lumped in groups representing higher-level taxa or individual prey types with high contributions. Items with low contributions were grouped as 'others'.

Cluster analysis revealed two distinct species groups at a distance (in Bray-Curtis space) of ca. 45 (Fig. 3). A first cluster contained five fishes of the Sciaenidae family (*M. ancylodon, C. jamaicensis, S. rastrifer, C. virescens, N. microps*) and one ray species (*G. micrura*). They are referred to as epi-piscivores because one-way SIMPER analysis revealed their diet was characterized by a combination of Pisces sp. and *Xiphopenaeus kroyeri* (Table 3). The other species cluster was taxonomically more diverse, including two sciaenids (*Paralonchurus brasiliensis* and *S. microps*), two flatfishes (*A. achirus, Symphurus plagiusa*), one ray (*D. guttata*), one catfish (*Amphiarius rugispinis*)

and one gurnard (*P. punctatus*). They are termed benthivores, with polychaetes and brachyurans being the main components of their diet. Both cluster groups, further referred to as trophic guilds, had high contributions of 'digested debris', especially the benthivores (Table 3).

Whereas epi-piscivores had a significantly higher average fullness index (Pseudo-F=40.6; p=0.0001), dietary diversity in terms of S (Pseudo-F=101.2; p=0.0001) and H' (Pseudo-F=51.2; p=0.0001) was significantly higher for the benthivores (Table 3).

PCO analysis (Fig. 4) confirmed the segregation of fishes in two trophic guilds along the first axis, which explained 53 % of the variation observed in the diet of the different species. Along the second axis, the epi-piscivores were more variable than the benthivores, related to a diet dominated by *X. kroyeri* (*C. virescens* and *N. microps*), or rather Pisces sp. (notably *G. micrura*).

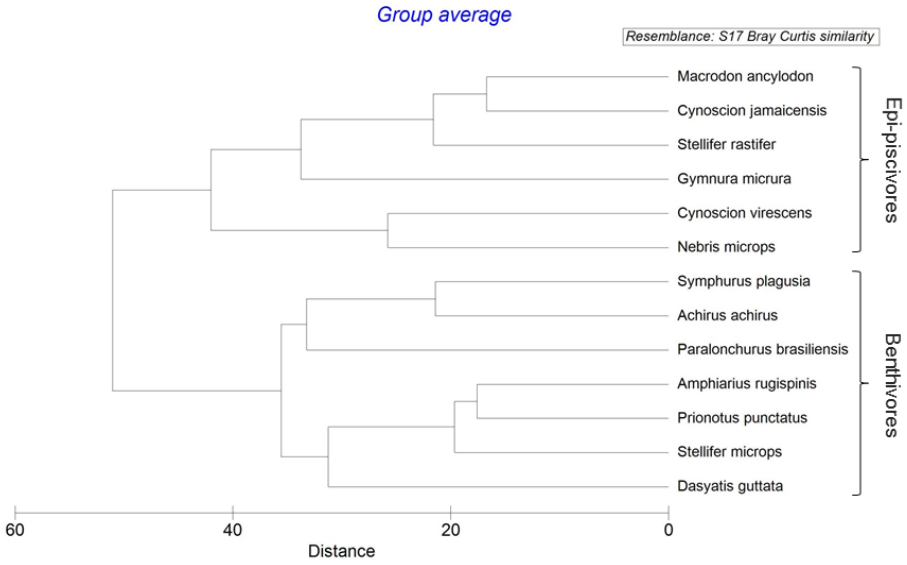

Figure 3. Group-averaging cluster based on the distances among centroids for the grouping factor 'species', calculated from a resemblance matrix with Bray-Curtis similarities among samples (stomachs). At a distance (in Bray-Curtis space) of ca. 45, two species clusters (trophic guilds) are distinguished.

Table 3. Characterization of the two trophic guilds as identified by cluster analysis. The fish species constituting each guild are listed, together with the prey types accounting for 90 % cumulative contribution to the diet of each trophic guild. For each prey type the contribution to 'within-group' similarity, based on one-way SIMPER analysis of arcsine transformed relative gravimetrical stomach content data is given (Contr%), together with the average (±SD) gravimetrical fraction of the diet (Grav%). Further, average (±SD) fullness index (FI), diet species richness (S) and Shannon diversity (H') are listed.

Benthivores	Epi-piscivores
Achirus achirus	*Cynoscion jamaicensis*
Amphiarius rugispinis	*Cynoscion virescens*
Dasyatis guttata	*Gymnura micrura*
Paralonchurus brasiliensis	*Macrodon ancylodon*
Prionotus punctatus	*Nebris microps*
Stellifer microps	*Stellifer rastrifer*
Symphurus plagiusa	

Prey group	Contr%	Grav%	Prey group	Contr%	Grav%
Digested debris	87.9	55.9 ± 34.4	Pisces sp.	39.1	29.9 ± 42.8
Polychaeta sp.	3.5	9.8 ± 2.3	Digested debris	27.9	24.7 ± 38.5
Brachyura sp.	2.9	8.8 ± 2.1	*Xiphopenaeus kroyeri*	17.6	19.5 ± 35.1
			Decapoda sp.	13.4	17.3 ± 34

FI	0.2 ± 0.3	0.9 ± 2.4
S	2.9 ± 1.6	1.9 ± 1
H'	0.7 ± 0.5	0.5 ± 0.5

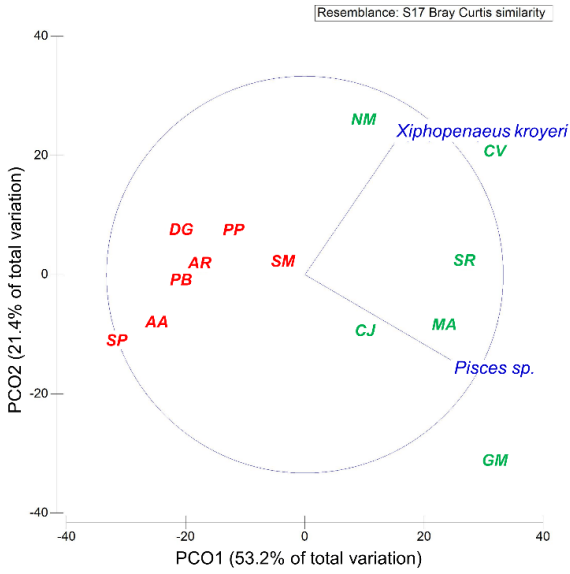

Figure 4. Principal coordinates (PCO) analysis ordination plot based on the distances among centroids for the grouping factor 'species', calculated from a resemblance matrix with Bray-Curtis similarities among samples (stomachs). The two trophic guilds as identified by cluster analysis are indicated with colors: benthivores in red, epi-piscivores in green. Two main prey types (*X. kroyeri* and Pisces sp.) are overlaid as vectors using multiple correlation (r >0.3; with respect to the circle representing 1). AA=*Achirus achirus*, AR=*Amphiarius rugispinis*, CJ=*Cynoscion jamaicensis*, CV=*Cynoscion virescens*, DG=*Dasyatis guttata*, GM=*Gymnura micrura*, MA=*Macrodon ancylodon*, NM=*Nebris microps*, PB=*Paralonchurus brasiliensis*, PP=*Prionotus punctatus*, SM=*Stellifer microps*, SR=*Stellifer rastrifer*, SP=*Symphurus plagiusa*

3.2 SI ANALYSES

3.2.1 COMPARISON AMONG SPECIES AND LENGTH CLASSES

The C SI composition of the 13 investigated fishes (Annex 5.2) was significantly influenced by the interaction term 'species x length class' (Pseudo-F=76.7; p=0.0001). Within each length class, the C SI composition differed significantly among most fish species (Annex 5.3). In the eight species for which multiple length-classes were sampled, the C SI composition of length-class S, L and XL differed significantly except for the difference between S and L in *M. ancylodon, C. virescens* and *D. guttata*.

The N SI composition of the 13 investigated fishes (Annex 5.2) was also significantly influenced by the interaction term 'species x length class' (Pseudo-F=870.2; p=0.0001). Within each length class, the N SI composition differed significantly among most fish species (Annex 5.3). In the eight species for which multiple length-classes were sampled, the N SI composition of length-class S, L and XL differed significantly except for the difference between S and L in *P. punctatus* and *D. guttata*.

PREDATION ON *XIPHOPENAEUS KROYERI*

The isotopic niche of the demersal fish community, represented by its standard ellipse area (SEA_c), ranged from ca. -15.5 to -14.5 in $\delta^{13}C$ and 11.5 to 13.5 in $\delta^{15}N$ (Fig.5). The fish community SEA_c overlapped for 20% with the theoretical SEA_c *X. kroyeri* consumer, which fell almost entirely (for 98%) within the fish community SEA_c (Fig.5).

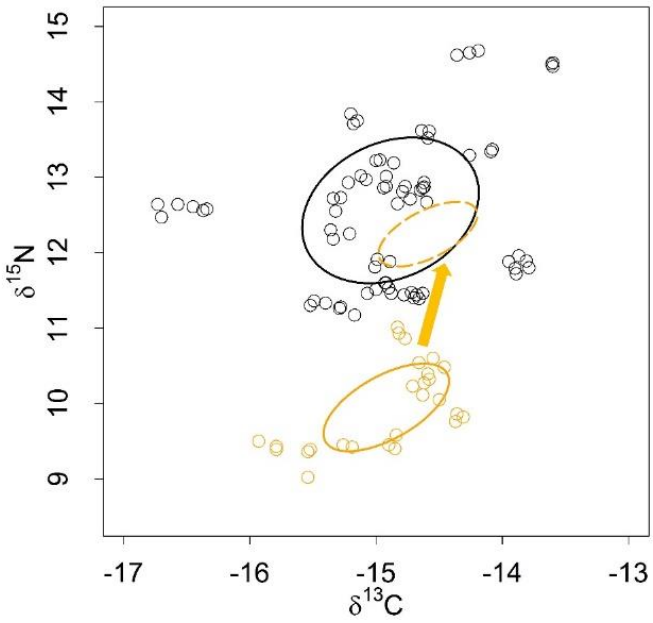

Figure 5. C-N biplot of stable isotope compositions of 13 demersal fishes (black circles; this study) and *Xiphopenaeus kroyeri* (orange circles; Willems et al., submitted a). Lines enclose standard ellipse areas (SEA_c), representing the isotopic niches of the demersal fish community (black line) and *X. kroyeri* (solid orange line). The theoretical SEA_c of a *X. kroyeri* consumer (i.e. after isotopic fractionation; orange arrow) is represented by the dashed orange line.

Upon closer inspection, the theoretical SEA_c of a consumer of *X. kroyeri* juveniles and postlavae overlapped with the SEA_c of large *C. virescens,* and was in close vicinity to the SEA_c's of small *N. Microps* and *C. virescens* on the biplot. The theoretical SEA_c of an adult *X. kroyeri* consumer did not show overlap with any fish SEA_c (Fig. 6).

Fish species showed a high degree of overlap in their $\delta^{13}C$ values (Fig. 7). Further, the $\delta^{13}C$ composition of all but two (*P. punctatus* and *A. achirus*) demersal fishes fell within the range of $\delta^{13}C$ composition of *X. kroyeri*. In contrast, prey group 1 and 2 had more depleted $\delta^{13}C$ values, which only showed overlap with the $\delta^{13}C$ values of *P. punctatus* (Fig.7).

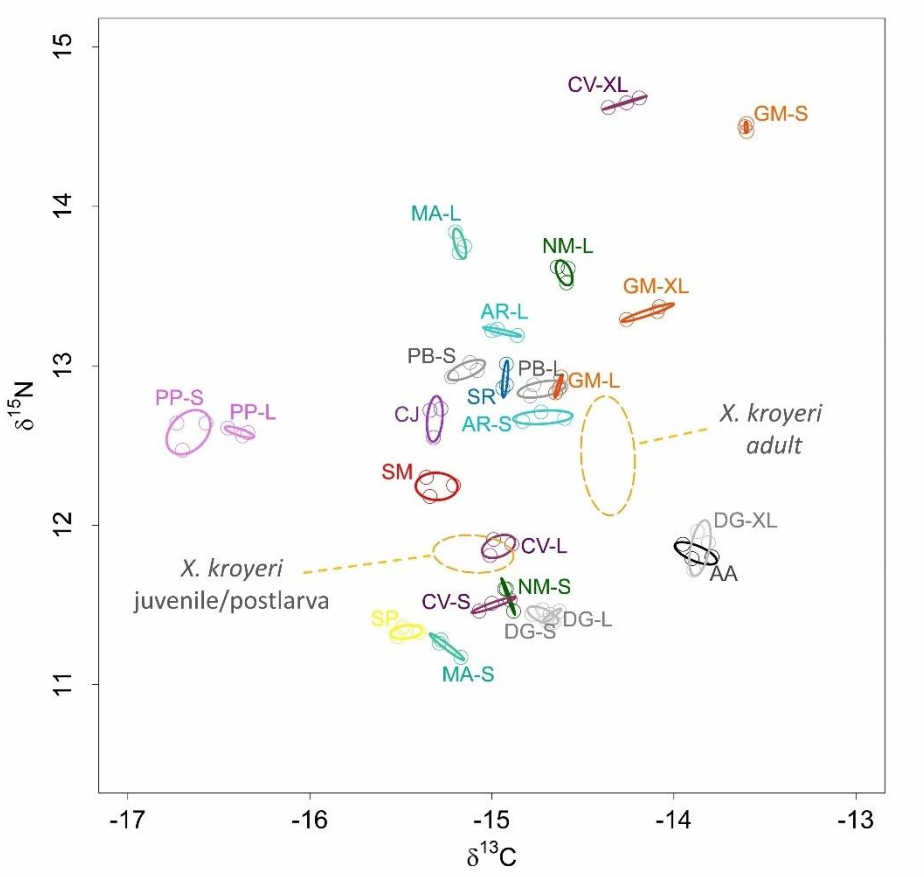

Figure 6. C-N biplot of demersal fish stable isotope compositions. Lines enclose standard ellipse areas (SEA_c), representing the isotopic niches of the different species and length classes (solid lines). Orange dashed lines represent the theoretical isotopic niches of consumers of *Xiphopenaeus kroyeri* adults and juveniles/postlarvae and adults. *AA=Achirus achirus, AR=Amphiarius rugispinis, CJ=Cynoscion jamaicensis, CV=Cynoscion virescens, DG=Dasyatis guttata, GM=Gymnura micrura, MA=Macrodon ancylodon, NM=Nebris microps, PB=Paralonchurus brasiliensis, PP=Prionotus punctatus, SM=Stellifer microps, SR=Stellifer rastrifer, SP=Symphurus plagiusa.*

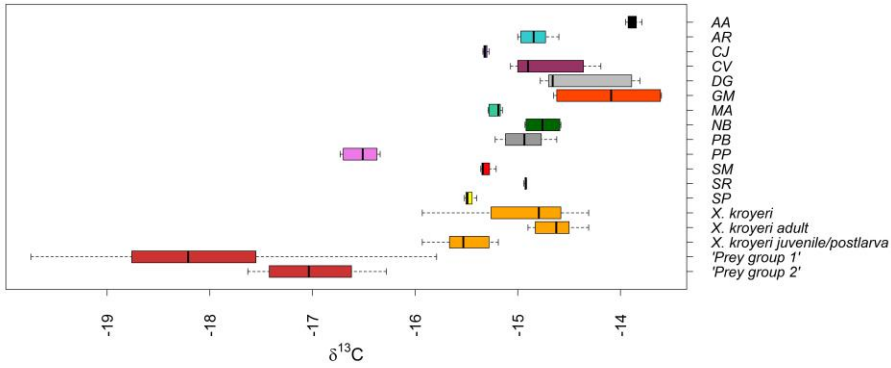

Figure 7. Box-and-whisker plots showing minimum, maximum, 0.25 percentile, 0.75 percentile and median $\delta^{13}C$ values of 13 demersal fish species, *Xiphopenaeus kroyeri*, prey group 1 (hyperbenthic and planktonic copepods, bivalves, brachyurans, brachyuran zoeae larvae, macrobenthic amphipods, *Lucifer faxoni*) and prey group 2 (hyperbenthic amphipods, sipunculids, fish larvae, chaetognaths, polychaetes, *Acetes sp.*). *AA=Achirus achirus, AR=Amphiarius rugispinis, CJ=Cynoscion jamaicensis, CV=Cynoscion virescens, DG=Dasyatis guttata, GM=Gymnura micrura, MA=Macrodon ancylodon, NM=Nebris microps, PB=Paralonchurus brasiliensis, PP=Prionotus punctatus, SM=Stellifer microps, SR=Stellifer rastrifer, SP=Symphurus plagiusa.*

4 DISCUSSION

The mid-trophic level in the benthic food web of the inner Suriname Shelf is dominated by *X. kroyeri* (Willems et al., 2015b), which feeds on a variety of lower trophic level food sources (Willems et al., submitted a). The present study reveals that the shrimp itself constitutes an important food source for demersal fishes higher in the food chain. We therefore hypothesize that *X. kroyeri* fulfills a key trophic role, through which energy is channeled up the food chain in a 'wasp-waist' pattern.

4.1 *XIPHOPENAEUS KROYERI* AS 'WAIST'?

Xiphopenaeus kroyeri is the only abundant epibenthic species occurring up to 27m depth on the Suriname Shelf. The species contributes 74% to the similarity within the species-poor coastal epibenthic assemblage, where it reaches densities up to 1383 individuals per 1000 m^2 (Willems et al., 2015b). Few other epibenthic species live on the muddy nearshore seabed, and the macro-infauna, generally a major food source for demersal fishes (e.g. Gibson and Ezzi, 1987; Powers et al., 2005), is scarce (Swennen et al., 1982; ESC, 2011; Willems et al., 2015b).

A variety of food sources from the lowest trophic levels contribute to the diet of *X. kroyeri* off Suriname (Willems et al., submitted a). In agreement with other diet studies (Cortés and Criales, 1990; Branco and Junior, 2001), the species

was found to consume over 20 different prey taxa, mainly small hyperbenthic crustaceans. But benthic microalgae on intertidal mudflats were found to be a major food source for *X. kroyeri* as well (Willems et al., submitted a). Through opportunistic feeding, the shrimp thus accumulates multiple low trophic level food sources, comprising both primary and secondary producers.

Higher up in the food chain, demersal fishes are typical predators of penaeid shrimp on tropical shelves (e.g. Salini et al., 1994; Brewer et al., 1995; Manickchand-Heileman et al., 1998). In contrast to the epibenthos (Willems et al., 2015b), the demersal fish community on the inner Suriname Shelf is quite diverse: up to 34 m depth, at least 85 demersal fish species are known to occur (Willems et al., 2015a). The present study shows that *X. kroyeri* is a major food source for these higher trophic level fishes. The 'wasp-waist' pattern in species diversity at different trophic levels therefore seems to reflect an important mechanism of trophic control, in which energy passes through a single species, *X. kroyeri*.

We investigated the trophic importance of *X. kroyeri* for 13 demersal fish species, representing the most common species (Willems et al., 2015a). Their combined diet was considered a good proxy for the entire demersal fish community. Eleven of the 13 fishes had *X. kroyeri* in their stomachs. Dual SI analysis confirmed the trophic importance of *X. kroyeri*: the fish community isotopic niche overlapped considerably with the theoretical isotopic niche of a *X. kroyeri* predator. Calculating overlap with theoretical isotopic niches is not one of the standard analytical methods in stable isotope ecology (e.g. Layman et al., 2012). Yet it is a straightforward combination of concepts of isotopic fractionation (e.g. Vander Zanden and Rasmussen, 2001; Post, 2002) and isotopic niche overlap (Layman et al., 2007; Jackson et al., 2012). Irrespective of the way they are analysed, stable isotopes provide information regarding the flow of energy through food webs (Layman et al., 2012). While the contribution of prey to consumers is mostly estimated using SI mixing models (e.g. Phillips et al., 2005; Parnell et al., 2010), such models should be well-informed on all potential food sources and incorporate their SI compositions (Phillips et al., 2014), which was not feasible in the current study. We did however consider several hyper- and macrobenthic taxa (prey group 1 and 2) for which SI composition data were available from the study area (Willems et al., submitted a). Their median $\delta^{13}C$ composition was depleted by 2-3 ‰ compared to *X. kroyeri,* indicating that these prey taxa were of little trophic importance for most demersal fishes.

Xiphopenaeus kroyeri was the only shrimp species frequently encountered in the stomachs. Hence, many 'shrimp-like Decapoda sp.' were probably also *X. kroyeri* specimens for which digestion state did not permit identification. When including shrimp-like Decapoda sp. in calculating the feeding coefficient (including postlarval stages), Q equaled 316.7, indicating *X. kroyeri* is a preferential prey for the demersal fish community. Except for Pisces sp. and

'digested debris', all other prey types had Q values <200, classifying them as either secondary or accidental prey (Hureau, 1970). Further evidence for the trophic importance of *X. kroyeri* came from its SURF score, identifying key food web components upon which higher trophic levels depend (Plaganyi and Essington, 2014). While 'digested debris' and Pisces sp. also had SURF scores >0.001, these prey types did not represent single species. Therefore, according to the SURF methodology, only *X. kroyeri* categorizes as a true 'key prey species' (Plaganyi and Essington, 2014).

Considering the individual fish species, both stomach content and SI analysis showed that they all had a slightly different trophic ecology. Nevertheless, fishes could be grouped in two feeding guilds: the epi-piscivores and the benthivores. The epi-piscivores were mainly sciaenid fishes with oblique mouths and sharp teeth (e.g. Léopold, 2005), suggesting a feeding ecology as predators of epibenthos and fish. Within this feeding guild, we observed a dichotomy with on the one hand *Cynoscion jamaicensis*, *M. ancylodon* and *S. rastrifer* feeding on a combination of fish and shrimp (confirmed as well by Muto et al., 2014; Willis et al., 2015; Camargo and Isaac, 2004; Pombo et al., 2013), and *G. micrura* which preyed almost exclusively on fish, as also reported in Yokota et al. (2013). On the other hand *N. microps* and *C. virescens* were primarily feeding on shrimp, and more specifically on *X. kroyeri*. These sciaenid fishes are indeed known as predators of penaeid shrimp (Lowe-McConnell, 1966; Muto et al., 2014). Moreover, their isotopic niche was very similar to the theoretical isotopic niche of a predator of *X. kroyeri* juveniles and postlarvae. Based on mean carapace length (Castro et al., 2005), most *X. kroyeri* encountered during the stomach analyses were juveniles indeed. Postlarvae occurred regularly in the stomachs of *N. microps* and *C. virescens* as well (Annex 5.1). As such, a remarkable congruence was observed between our results from stomach content and SI analysis for *N. microps* (S) and *C. virescens* (S & L). This validates the use of the isotopic fractionation equations for fish muscle tissue reported by Caut et al. (2009).

The second trophic guild, the benthivores, were a taxonomically more diverse group of fishes than the epi-piscivores, which nevertheless all were morphologically adapted to bottom feeding (e.g. Léopold, 2005). They had a wider trophic niche compared to the epi-piscivores, evidenced by their higher mean values of dietary species richness and Shannon diversity. Further, the benthivorous fishes spanned a wider range of $\delta^{13}C$ values, indicating a more variable diet in terms of carbon sources (Fry, 2006). Low average fullness indices (Berg, 1979; Hyslop, 1980), and high gravimetrical contributions of digested debris indicated food in the stomachs of the benthivores was often in an advanced state of digestion. Therefore, most benthivorous fishes had not been feeding recently when caught during daytime, suggesting these species primarily feed at night. Based on the texture and whitish color, fish and shrimp were the most likely sources of digested debris in the stomachs (K. Hostens, pers. comm.). Except for *A. achirus*, *X. kroyeri* was encountered in the stomachs

of all benthivores, most of which have also been reported to feed on decapod crustaceans (e.g. Melo and Teixeira, 1992; Soares et al., 1998; Soares and Vazzoler, 2001; Carvalho Neta and de Almeida, 2001; Muto et al., 2014). Further, the $\delta^{13}C$ composition of most benthivores overlapped to some extent with the $\delta^{13}C$ composition of *X. kroyeri*. For these reasons, our study might have underestimated feeding on *X. kroyeri* by the benthivores.

In conclusion, the current study showed that *X. kroyeri* is a major food source for the demersal fish community on the inner Suriname Shelf. It contributed to the diet of nearly all investigated fish species, and most likely it is also an important prey for many other demersal fishes not included in our analyses. Whereas *X. kroyeri* is mainly preyed upon by epi-piscivores, fish species from this trophic guild dominate the demersal fish community on the inner Suriname Shelf in terms of densities and, because of their larger mean size, also in terms of overall biomass (Willems et al., 2015a). *Xiphopenaeus kroyeri* might therefore locally constitute a key prey species for higher trophic level demersal fishes. Together with the fact that this shrimp species itself accumulates a variety of low-trophic level food sources (Willems et al., submitted a), the results of our study support the hypothesis that *X. kroyeri* is most likely a 'waist' species through which energy is channeled up the food chain in the benthic food web of the inner Suriname Shelf.

4.2 MANAGEMENT IMPLICATIONS

In the productive nearshore waters of the Suriname Shelf, *X. kroyeri* seems to fulfill a role which is functionally similar to small pelagic fishes in upwelling systems. *Xiphopenaeus kroyeri* is a fast growing and short lived crustacean (Branco et al., 1994; Heckler et al., 2013a), that establishes dense populations (Willems et al., 2015b). We found that it constitutes important prey for higher trophic level predators. Demersal fishes might therefore be competing for the same resource with fisheries for *X. kroyeri*.

Several of the fish species included in the current study are important target species for the coastal artisanal fishing fleet off Suriname. In particular, the shrimp-specialists *N. microps* and *C. virescens* are high-valued commercial fishes (Bhagwandin, 2012). Other important commercial target species that were not studied (e.g. C*. acoupa*, *C. similis* and *C. steindachneri*) have a very similar morphology to *C. virescens* (Léopold, 2005), and probably also highly depend on *X. kroyeri* as a food source. This validates concerns regarding food availability for commercially important demersal fishes, which have existed among the artisanal fishing communities since the start of *X. kroyeri* trawl fisheries off Suriname in the mid 1990's (M. Lall, pers. comm.). On the other hand, populations of large demersal (epi-piscivorous) fishes off Suriname are suppressed due to overexploitation by the coastal artisanal fishing fleet (Charlier, 2000). This might relieve top-down control on shrimp populations,

and allow for a sustainable exploitation of *X. kroyeri* without affecting food availability for fish. The relative importance of these interactions is unknown and should further be explored through ecosystem modelling, in order to define optimal effort levels to maximize fisheries yields of both *X. kroyeri* and demersal fish. So far, a precautionary approach is advisable, using a risk-based management scheme that effectively reduces fishing effort for *X. kroyeri* when there are indications that the species becomes scarcer (Essington et al., 2015).

Fisheries for invertebrates, including bivalves, crustaceans, cephalopods and echinoderms have expanded substantially, with global catches having increased six fold over the past 60 years (Anderson et al., 2011; Eddy et al., 2015). Our study shows that some of the targeted invertebrates may be key prey species in coastal benthic ecosystems. Consequently, their overexploitation can have substantial effects on the productivity and recovery of species higher in the food web (Smith et al., 2011). 'Wasp-waist' trophic control is likely more widespread than previously assumed, and should be considered in the management of fisheries for benthic invertebrates as well.

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PART III

IMPACT OF *XIPHOPENAEUS KROYERI* TRAWL FISHERIES ON THE COASTAL ECOSYSTEM OF SURINAME

6

CATCH COMPOSITION IN SEABOB SHRIMP *XIPHOPENAEUS KROYERI* TRAWL FISHERIES OFF SURINAME

Modified from:

Willems,T., De Backer, A., Vincx, M., Hostens, K. Catch composition in seabob shrimp Xiphopenaeus kroyeri *trawl fisheries off Suriname. In preparation.*

Catch composition in the trawl fishery for Atlantic seabob shrimp Xiphopenaeus kroyeri *off Suriname was assessed based on 68 catch samples. They were taken both during day and night on six commercial fishing trips between April and November 2014. Catch rate in the seabob fishery averaged 205 ± 180 kg of total catch per hour of trawling. Catches were dominated by seabob shrimp, accounting for 59 ± 13 % of the total catch by weight. The bycatch was dominated by fish (31 ± 14 % of total catch), followed by jellyfish (8 ± 10 %) and benthos (benthic invertebrates; 2 ± 3 %). Most of the bycatch was discarded. Retained bycatch represented 4% of the total catch, and included three commercial fish species (*Macrodon ancylodon, Cynoscion virescens *and* Nebris microps*), and brown shrimp* Penaeus subtilis*. Fish bycatch consisted of 54 species, dominated by representatives from the Sciaenidae. Two species,* Stellifer microps *and* Cynoscion jamaicensis *represented 50% of the fish bycatch by weight, and occurred in each haul. Most fishes in the bycatch were small, measuring some 10 cm. Bycatch of benthos included 24 benthic invertebrate taxa, dominated by* P. subtilis*, the gastropod* Marsupina bufo *and the swimming crab* Callinectes ornatus*. Further, overall catch rate and relative catch composition differed significantly among months. Highest catch rates were observed in August, but this month also had the highest bycatch ratios. Little diurnal variability in overall catch rate and catch composition was observed. In general, the Suriname seabob fishery produces relatively low bycatch ratios for a tropical penaeid shrimp fishery. Nevertheless, discarded bycatch includes species of commercial interest for the coastal artisanal fishing fleet, notably* C. jamaicensis*,* C. virescens, M. ancylodon *and* N. microps*. Further, several elasmobranch species of conservation concern are caught, including five species of rays and the electric ray* Narcine bancroftii*. In the absence of population estimates of the bycaught species, we recommend the fishery to undertake further efforts to reduce bycatch, in order to minimize negative socio-economic and ecological effects of bycatch mortality.*

1 INTRODUCTION

Shrimp are a highly valued seafood product, accounting for 16% of the total value of internationally traded fishery exports (Gillett, 2008). Despite the growing contribution of aquaculture, the majority (60%) of global shrimp production originates from fisheries, mainly (for about 70%) in tropical and subtropical areas (FAO, 1999). Tropic shrimp are mainly caught by bottom otter-trawling. Although efficient in catching the targeted shrimp, it is a 'catch-all' technique which produces high amounts of non-target catch (henceforth 'bycatch') (Eayrs, 2007). Much of this bycatch consists of small and low-value 'trash fish' and invertebrates, which are discarded (henceforth 'discards') (Andrew and Pepperell, 1992; Gillett, 2008). Bycatch in tropical shrimp trawling might also include species of conservation concern, notably elasmobranchs and sea turtles (e.g. Shepherd and Myers, 2005; Griffiths et al., 2006).

Bycatch, particularly when discarded, is a serious concern for a number of reasons. First, discards often remain unreported, which hampers a proper assessment of the status and trends of the discarded species. Second, bycatch in one fishery might constitute target catch for other fisheries in the same area, creating interactions among fleets that complicate management. Third, like target catch, bycatch affects the overall structure of trophic webs and living habitats. Finally, bycaught fish is often dead when discarded, which raises the ethical issue of wastage of natural resources (Gillett, 2008). Addressing these problems related to bycatch and discards is therefore an essential part of the application of an 'Ecosystem Approach to Fisheries' (EAF) in shrimp trawling (Garcia et al., 2003; Garcia and Cochrane, 2005; Gillett, 2008).

Off the coast of Suriname, shrimp trawlers target Atlantic seabob shrimp *Xiphopenaeus kroyeri* (Crustacea: Penaeidae). Seabob is a rather small penaeid shrimp that is widely distributed in estuarine and shallow nearshore waters of the Western Atlantic (Holthuis, 1980; Costa et al., 2007; Freire et al., 2011) and one of the top ten most caught penaeid shrimps in the world (Silva et al., 2013; FAO, 2014a). With an annual production of 8,000 to 10,000 tons, Suriname is the country with the third highest global production of Atlantic seabob shrimp (FAO, 2014a).

In the Suriname seabob fishery, concerns have been raised on both the socio-economic and environmental impact of bycatch. First, on the socio-economic side, seabob trawling might interact indirectly with artisanal fisheries, the most import fishing sector in Suriname, both in terms of employment and landings (Bhagwandin, 2012). While both fisheries are spatially segregated (LVV, 2010), the demersal fish species targeted by the artisanal fleet are known to occur in the bycatch of seabob fisheries (Polet et al., 2010; Southall et al., 2011), invoking a competition for the same resource. Second, on the environmental impact side, bycatch might affect the structure of benthic communities of fish and invertebrates on the Suriname Shelf. Notably, the mortality of several species

of rays (Elasmobranchii: Batoidea) known to occur in the seabob bycatch might be problematic (Southall et al., 2011). Due to their live history, elasmobranchs are generally vulnerable to fishing mortality (Stevens et al., 2000) and several threatened species occur in the area (Willems et al., 2016).

Seabob trawl fisheries in Suriname have addressed bycatch problems by equipping all trawls with Turtle Excluder Devices (TEDs) (since 1999) and square-mesh panel Bycatch Reduction Devices (BRDs) (since 2009; LVV, 2010). TEDs have reduced the bycatch of sea turtles to nearly zero (S. Hall, pers. comm.). While small rays are still caught, TEDs have also proven efficient in excluding large-sized ray species from the trawls (Willems et al., 2016). BRDs, on the other hand, have shown to cause a 34%-reduction in fish bycatch (by weight) (Polet et al., 2010). Over the years, some information has been gathered through a sea-going observer program by the Fisheries Department of the Suriname Ministry for Agriculture, Livestock and Fisheries (LVV). This data has been reviewed during the assessment of the Suriname seabob fishery against the Marine Stewardship Council (MSC) Principles and Criteria for Sustainable Fisheries in 2011 (Southall et al., 2011). The assessment concludes that, on average, 69% of the bulk catch weight comprises seabob, while 19% of the catch weight is retained bycatch and 12% is discarded bycatch (Southall et al., 2011). Retained bycatch includes 3 species of fish, which are retained from a minimum length of ca. 25 cm: King weakfish *Macrodon ancylodon*, Green weakfish *Cynoscion virescens* and Smalleye croaker *Nebris microps*. Further, bycatch of Brown shrimp *Penaeus subtilis* is sorted from the seabob shrimp and landed separately (J. Jagroop and S. Hall, pers. comm.). The Suriname seabob fishery seems to produce low amounts of bycatch for a tropical shrimp fishery (e.g. Andrew and Pepperell, 1992; EJF, 2003; Gillett, 2008). Nevertheless, detailed information on the species being caught and their length distribution is largely lacking, hampering well-informed ecosystem-based management decisions.

The aim of the current study was to provide detailed and up-to-date information on catch composition in the Suriname seabob trawl fishery in order to quantify target catch versus bycatch. Based on samples from commercial hauls in 2014, bycatch-to-shrimp ratios are calculated, and catch rates and length-distributions of bycatch species are presented. This information can be used for further assessment and mitigation of both socio-economic and environmental effects of seabob trawling in Suriname.

2 MATERIALS AND METHODS

2.1 STUDY AREA

The study was conducted on commercial fishing grounds for seabob shrimp (6.22°N to 6.57°N and 54.16°W to 55.16°W) on the continental shelf off Suriname (FAO Statistical area 31). The area is characterized by mud and sandy mud substrates (Willems et al., 2015b) and water depth ranges from 25 to 35 m (Fig. 1). Commercial shrimp fishing activity occurs year-round in this area (Pérez, 2014). The nearshore waters off Suriname are severely influenced by river discharge, mainly from the Amazon River. Most rainfall in Suriname, and peak discharge of both the Amazon and local rivers, occurs between December and July (Amatali, 1993, Hu et al., 2004). From August to November, input of (Amazon) river discharges in the nearshore waters of Suriname is lower. This is also a period with reduced northeast trade winds causing calm and warmer sea surface waters (Amatali, 1993; Augustinus, 2004).

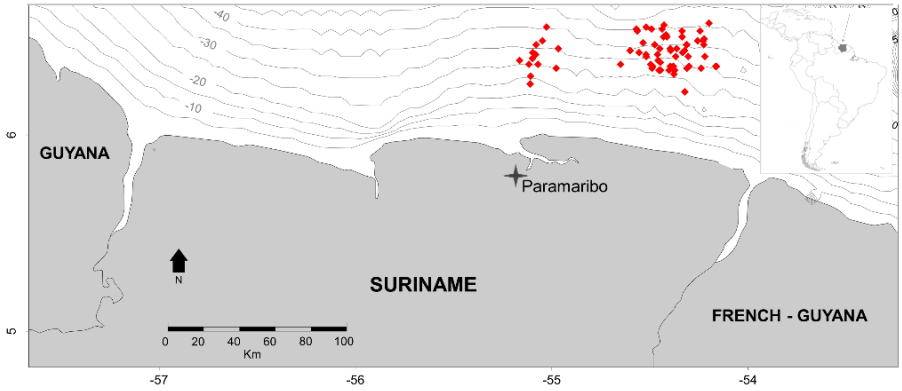

Figure 1. Map of the inner continental shelf of Suriname. The start locations of the 68 sampled commercial fishing hauls are indicated with red symbols.

2.2 TECHNICAL AND OPERATIONAL CHARACTERISTICS OF THE FISHERY

Vessels in the Suriname seabob trawling fleet are equipped for twin-rig bottom-trawling, which involves dragging two trawls attached to two steel-footed wooden doors and a sledge at either side of the vessel, resulting in two port- and two starboard-codends (and therefore also referred to as quad-rig trawling) (Southall et al., 2011) (Fig. 2). The trawls have a vertical opening of ca. 2 m and tickler chains attached to the footrope. Mesh size of the trawls ranges from 57 mm in the body and wings of the trawl to 45 mm in the codend. Each trawl is fitted with an aluminium super-shooter TED with a bar spacing of 10 cm, installed in a downward-excluding configuration. Trawls are also fitted with

a square-mesh-panel BRD (11 x 11 meshes, 15 cm stretched mesh size) inserted ca. 40 cm behind the TED in the upper side of the codend (Willems et al., 2016). To avoid direct interaction with other fishing fleets, seabob trawling is only allowed in an area delimited by the 18 and 27 m depth contours (up to 33 m in the eastern part of the shelf) (LVV, 2010). The inshore waters are used by the artisanal fishing fleet, which targets demersal finfish with gillnets, while commercial fisheries for fish and shrimp operate in the offshore waters beyond 27 - 33 m depth (Bhagwandin, 2012).

The seabob fishery operates around the clock, making hauls that last 3-4 hours, at a speed of 2.5 to 3.5 knots (Pérez, 2014). A small trynet is dragged from the stern of the vessel to quickly and easily assess the potential catch of shrimp before fishing starts (Fig. 2). During a haul, the trynet is also periodically hauled (ca. every 30 minutes) to monitor shrimp catches, and if necessary adjust the vessel's course. When hauling the gear, the otter boards, the mid-trawl sledge and the nets remain suspended at the ends of the outriggers as the codends alone are taken aboard. The catch is dumped on the back deck, processed manually by three or four men and stored on ice below decks. Fishing trips typically last six to eight days, of which about two days may be spent steaming to and from the fishing grounds (Southall et al., 2011). Fishing trips consist of about 30 hauls and landings might be as high as 20 tonnes after a trip.

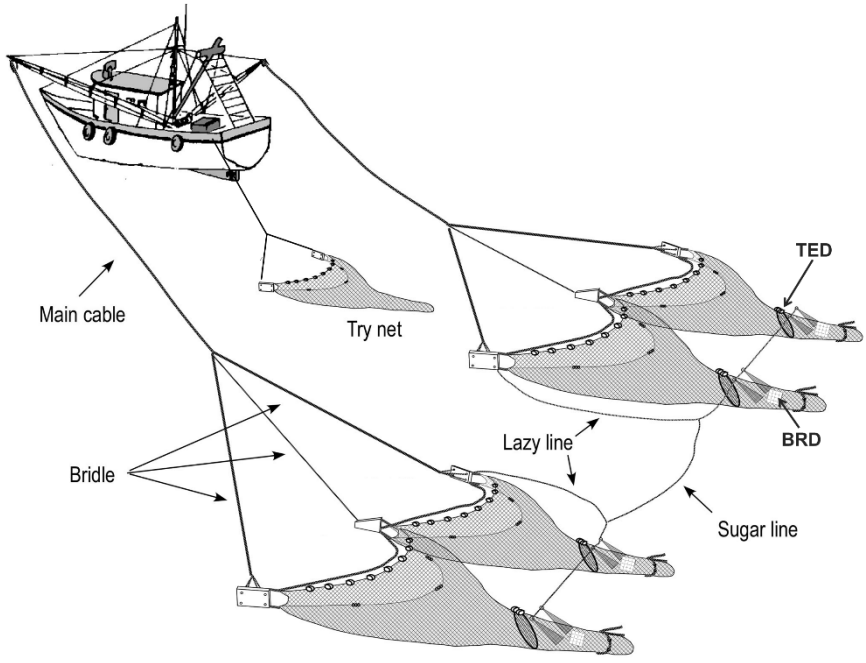

Figure 2. Net configuration in the Suriname seabob fleet: twin-rig otter trawls fished from outriggers and a try-net deployed from the stern. Each trawl is equiped with a Turtle Excluder Device (TED) and square-mesh panel Bycatch Reduction Device (BRD) (Adapted from Scott-Denton et al., 2010).

2.3 CATCH SAMPLING

Bycatch data were collected on six commercial fishing trips onboard FV *Neptune-6* in the period April – November 2014 (Table 1). During each trip, catch samples were obtained from every haul during 2 to 4 consecutive days of fishing. In total, 68 hauls were sampled. For each haul, start and end time, start position and start depth were noted from the vessels instruments. No depth measurements could be taken in October. Upon retrieval of the trawls, the catch from all four codends was dumped simultaneously on deck. Large organisms that were unlikely to end up in the catch subsample (e.g. large stingrays) were first sorted from the total catch, identified and measured to the nearest centimetre. Next, the catch was homogenized with shovels and a subsample of a full or half basket (40 resp. 20 L) was taken, depending on the available manpower to process the subsample.

The subsample was broken down in four components including shrimp (the target catch) and three bycatch components: fish, jellyfish and benthos (epibenthic invertebrates such as crabs, starfish, molluscs, etc.). Bycaught *Penaeus sp.* shrimp were also classified as benthos. Shrimp, the target catch, consisted primarily of seabob shrimp *Xiphopenaeus kroyeri* but also included whitebelly shrimp *Nematopalaemon schmitti.* This small shrimp species sometimes occurs in small amounts among the seabob shrimp, and is not separated from it by the crew when processing the catch. The volume (0.1 L precision) and weight (0.1 kg precision) of the shrimp fraction was determined before the shrimp were returned to the crew for further processing. The three bycatch components were processed as follows. After weighting (0.1 kg precision) the fish fraction, all fishes were sorted per species and measured to the nearest centimetre (total length for finfish, disc width for rays). For the jellyfish fraction, only the weight (0.1 kg precision) was determined, as jellyfishes were often fragmented and could not be counted. Although different species of jellyfish were observed, they were not identified to species level and further analysed as 'jellyfish'. The benthos (benthic invertebrates) fraction was not processed on board but stored on ice in plastic bags and identified and weighted per species (0.1 g precision) upon return in the lab. After the total catch was processed by the crew, the total catch volume of shrimp was estimated by counting the number of processed baskets of shrimp for each haul.

Table 1. Overview and details on the sampled hauls.

	Month	Start Date	Start Time	End Time	Day/Night	Trawling Time (hours)	Start Latitude	Start Longitude	Depth (m)
1	April	2/04/2014	8:30	12:00	day	3:30	6.475	-55.048	24.4
2	April	2/04/2014	12:20	16:00	day	3:40	6.439	-54.967	23.8
3	April	2/04/2014	4:10	8:10	night	4:00	6.358	-55.117	24.7
4	April	3/04/2014	3:50	8:00	night	4:10	6.503	-54.414	27.1
5	April	3/04/2014	8:20	11:00	day	2:40	6.540	-54.569	28.3
6	April	3/04/2014	12:00	15:00	day	3:00	6.550	-54.519	28.7
7	April	3/04/2014	15:22	18:30	day	3:08	6.495	-54.336	28.7
8	April	4/04/2014	3:40	7:20	night	3:40	6.489	-54.224	28.3
9	April	4/04/2014	7:50	10:40	day	2:50	6.457	-54.312	28.7
10	April	4/04/2014	11:08	14:49	day	3:41	6.478	-54.228	28.3
11	May	22/05/2014	12:52	15:50	day	2:58	6.341	-54.382	22.9
12	May	22/05/2014	16:05	19:30	day	3:25	6.350	-54.381	22.3
13	May	22/05/2014	19:55	0:10	night	4:15	6.219	-54.322	21.9
14	May	23/05/2014	2:05	7:00	night	4:55	6.314	-54.378	23.5
15	May	23/05/2014	7:30	10:40	day	3:10	6.418	-54.334	23.2
16	May	23/05/2014	11:05	14:45	day	3:40	6.333	-54.403	23.5
17	May	23/05/2014	15:00	19:00	day	4:00	6.435	-54.323	23.5
18	July	13/07/2014	8:30	11:20	day	2:50	6.350	-54.161	18.3
19	July	13/07/2014	18:35	22:35	night	4:00	6.412	-55.082	18.9
20	July	13/07/2014	23:00	3:00	night	4:00	6.259	-55.110	18.9
21	July	14/07/2014	3:15	7:15	night	4:00	6.417	-55.097	19.8
22	July	14/07/2014	7:40	11:00	day	3:20	6.386	-55.098	20.1
23	July	14/07/2014	11:20	14:40	day	3:20	6.461	-55.080	20.4
24	July	14/07/2014	14:56	18:30	day	3:34	6.364	-55.071	21.0
25	July	14/07/2014	23:15	3:15	night	4:00	6.384	-55.164	18.9
26	July	15/07/2014	3:35	7:25	night	3:50	6.549	-55.027	20.7
27	July	15/07/2014	7:45	11:15	day	3:30	6.336	-54.978	19.2
28	July	15/07/2014	11:30	3:30	day	4:00	6.303	-55.108	18.9
29	August	23/08/2014	8:20	11:00	day	2:40	6.326	-54.453	21.6
30	August	23/08/2014	11:15	13:25	day	2:10	6.441	-54.397	23.2
31	August	23/08/2014	14:25	17:45	day	3:20	6.540	-54.492	21.0
32	August	23/08/2014	18:03	22:00	night	3:57	6.559	-54.428	21.3
33	August	23/08/2014	22:15	2:45	night	4:30	6.340	-54.489	20.7
34	August	24/08/2014	18:09	22:20	night	4:11	6.533	-54.564	21.0
35	August	24/08/2014	2:35	6:30	night	3:55	6.411	-54.520	22.3
36	August	24/08/2014	7:00	10:25	day	3:25	6.543	-54.438	20.7
37	August	24/08/2014	10:40	13:55	day	3:15	6.354	-54.486	20.7
38	August	24/08/2014	14:10	17:40	day	3:30	6.349	-54.396	21.6
39	August	25/08/2014	3:00	7:00	night	4:00	6.357	-54.496	21.9
40	August	25/08/2014	7:20	10:45	day	3:25	6.399	-54.519	21.9
41	August	25/08/2014	11:00	14:20	day	3:20	6.363	-54.650	20.7
42	August	25/08/2014	14:40	18:15	day	3:35	6.418	-54.556	21.3
43	August	25/08/2014	18:30	22:45	night	4:15	6.428	-54.601	21.6
44	August	25/08/2014	23:05	3:00	night	3:55	6.325	-54.446	20.7
45	October	6/10/2014	7:15	10:45	day	3:30	6.436	-54.364	N/A
46	October	6/10/2014	11:05	14:35	day	3:30	6.531	-54.336	N/A
47	October	6/10/2014	14:52	18:12	day	3:20	6.528	-54.245	N/A
48	October	6/10/2014	18:45	22:45	night	4:00	6.347	-54.165	N/A
49	October	6/10/2014	23:05	3:05	night	4:00	6.482	-54.257	N/A
50	October	7/10/2014	18:45	22:45	night	4:00	6.398	-54.220	N/A
51	October	7/10/2014	23:05	2:45	night	3:40	6.397	-54.369	N/A
52	October	7/10/2014	3:20	7:15	night	3:55	6.343	-54.239	N/A
53	October	7/10/2014	7:40	11:05	day	3:25	6.461	-54.314	N/A
54	October	7/10/2014	11:20	14:45	day	3:25	6.573	-54.199	N/A
55	October	7/10/2014	15:05	18:20	day	3:15	6.399	-54.305	N/A
56	October	8/10/2014	3:25	7:15	night	3:50	6.353	-54.301	N/A
57	October	8/10/2014	7:30	11:00	day	3:30	6.335	-54.374	N/A
58	October	8/10/2014	11:20	15:05	day	3:45	6.456	-54.226	N/A
59	October	8/10/2014	15:25	19:00	day	3:35	6.339	-54.312	N/A
60	November	17/11/2014	6:45	10:00	day	3:15	6.429	-54.394	24.1

Table 1. continued.

	Month	Start Date	Start Time	End Time	Day/Night	Trawling Time (hours)	Start Latitude	Start Longitude	Depth (m)
61	November	17/11/2014	10:20	13:45	day	3:25	6.378	-54.458	24.4
62	November	17/11/2014	14:05	17:20	day	3:15	6.470	-54.535	24.4
63	November	17/11/2014	17:40	22:30	night	4:50	6.411	-54.461	24.1
64	November	17/11/2014	22:48	3:00	night	4:12	6.510	-54.418	24.1
65	November	18/11/2014	3:20	7:10	night	3:50	6.496	-54.430	24.4
66	November	18/11/2014	7:30	11:00	day	3:30	6.442	-54.450	24.7
67	November	18/11/2014	11:15	14:45	day	3:30	6.372	-54.447	24.4
68	November	18/11/2014	15:05	18:30	day	3:25	6.456	-54.475	24.1

2.4 DATA ANALYSIS

First, the estimated volume of the total shrimp catch in each haul was converted to total weight based on equation [1], which was obtained from a regression of the volume versus weight measurements of the shrimp fractions in the 68 catch subsamples (Fig. 3):

$$\text{Shrimp weight} = 0.6633 * \text{Shrimp volume} + 0.7115 \quad [1]$$

with shrimp weight in kg and shrimp volume in L.

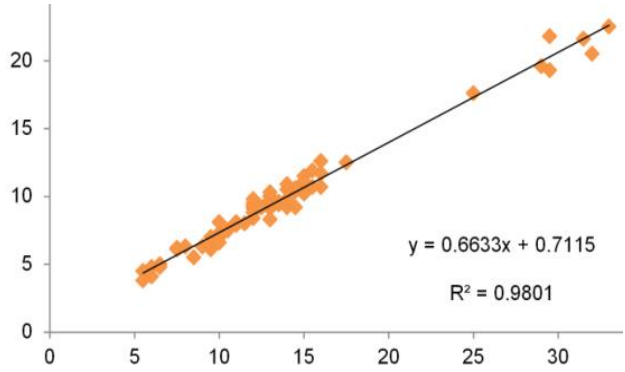

Figure 3. Scatterplot with trendline, equation and R^2 value of the volume and weight of the shrimp fraction in 68 catch samples (20 or 40 L) in seabob shrimp fisheries off Suriname.

2.4.1 BYCATCH CHARACTERIZATION

In order to (1) obtain average bycatch-to-shrimp ratios, and (2) calculate catch rates (catch-per-unit-effort) of the different bycatch fractions, the total weight of the bycatch fractions (fish, jellyfish and benthos) was calculated for each haul. This was done by extrapolating the ratios of the bycatch fractions in the catch subsample to haul level, hereby using the total shrimp catch, as follows:

$$Wbc = Pbc^{*} (Ws/Ps) \quad [2]$$

in which W_{bc} is the total weight (in kg) of the bycatch fraction (either fish, jellyfish or benthos), P_{bc} is the relative portion (by weight; ranging from 0 to 1) of the bycatch fraction in the catch subsample, W_s is the total shrimp catch weight and P_s is the relative portion (by weight; ranging from 0 to 1) of the shrimp fraction in the catch subsample (Andrew and Pepperell, 1992). Note that, to obtain the total weight of the fish fraction, the fish fraction weight as calculated using equation [2] was supplemented with the combined weight of large fishes sorted from the total catch. Their weight was calculated from the length measurement, using length-weight regressions available on FishBase (Froese and Pauly (Eds.), 2014) (see Annex Table A1).

Based on the total weights of the different catch fractions, bycatch – to – shrimp ratios were calculated for each haul, which were then used to calculate average (± SD) ratios (a method referred to as 'Ratio-Averager'; e.g. Pettovello, 1999; Ye, 2002). Further, weights of the catch fractions were recalculated to catch-per-unit-effort (CPUE; in kg/h) by dividing the total weight by the trawling time per haul (in hours).

Next, we calculated CPUE separately for each species of fish and benthos, both in terms of weight (kg/h) and numbers (#/h). To do so, first the total catch by weight was calculated for each species in each haul, based on the catch subsample. Whereas the weight per species of benthos in the subsample was measured directly, the weight per fish species in the subsample was calculated from the fish length-frequency-distributions, as follows:

1) Weight-at-length for each fish was obtained from the common length-weight regression:

$$W = a * L^{b} \quad [3]$$

in which W is fish weight (wet weight) and L is fish length (total length). The parameters *a* and *b* were obtained from FishBase (Froese and Pauly (Eds.), 2015), using average values at species level or, if unavailable, genus level (Annex 6.1).

2) For each fish species, the numbers per 1-cm length-class were multiplied with the weight-at-length for that length class. The total weight per species was obtained by summing the weights over all length-classes.

For each haul, total catch weight of each species of fish and benthos was then calculated from the weights in the catch subsample using equation [2]. Because upscaling from the subsample to the total catch was done based on weights, total numbers of fish and benthos per species could not be calculated in the same manner. Instead, for each species in each catch subsample, a

number-to-weight ratio was calculated. For each haul, this ratio was then applied to the total catch weight of each species, yielding the total number per species per haul.

Finally, the calculated catch weights per species were used to estimate the weight of retained bycatch. Based on own experience during sampling, and information from captains (J. Jagroop and S. Hall, pers. comm.), retained bycatch was defined as the combined weight of the fish species *M. ancylodon, C. virescens* and *N. microps* measuring >25 cm, and the weight of bycaught Brown shrimp *P. subtilis*.

2.4.2 VARIABILITY IN THE BYCATCH

Both temporal and diurnal variability in the bycatch was assessed, using the factors 'month' and 'day-night', respectively, in two separate one-way PERMANOVA analyses (Permutational ANOVA; Anderson et al., 2008). Based on average times of sunrise and sunset, hauls were classified as 'day' if they took place (for the major part) between 7:00h and 19:00h, and as 'night' otherwise (Table 1). Both PERMANOVA analyses were done on three different datasets. First, temporal and diurnal variability in total CPUE (shrimp + bycatch; in kg/h) was assessed based on an Euclidean distance resemblance matrix. Next, temporal and diurnal variability in the catch composition was assessed, based on a Bray-Curtis resemblance matrix of the relative composition of different catch fractions (shrimp, fish, jellyfish and benthos) per haul. Finally, temporal and diurnal variability in the 'bycatch community' was tested, including all fish and benthos species, and jellyfish (treated as one species). These tests were based on a Bray-Curtis resemblance matrix of the CPUE (in kg/h) per species per haul. The data on total CPUE and CPUE per bycatch species were square-root transformed prior to analysis, while the relative catch composition data were arcsine transformed (i.e. arcsine of square-root), which is appropriate for percentages and proportions (e.g. Jaworski and Ragnarsson, 2006).

Data analyses were performed in PRIMER v.6.1.13 with Permanova add-on software (Clarke and Gorley, 2006; Anderson et al., 2008). A significance level of p=0.05 was used in all tests. In the results, average values are reported with their standard deviation (SD).

3 RESULTS

3.1 BYCATCH CHARACTERIZATION

3.1.1 GENERAL CHARACTERISTICS

Hauls were done both day and night, and lasted 3:37 ± 0:28 hours on average. Average water depth during fishing was 22.8 ± 2.8 m. Catch rate (CPUE) averaged 205 ± 180 kg of total catch per hour of trawling. Catches were dominated by shrimp, the target catch, accounting for 59 ± 13 % of the total catch by weight. The bycatch was dominated by fish, representing 31 ± 14 % of the catch, followed by jellyfish (8 ± 10 %) and benthos (2 ± 3 %) (Fig. 4a). Accordingly, bycatch – to – shrimp ratios were all < 1 (Table 2). The majority of the bycatch included small and non-commercial fish, benthos and jellyfish, which was discarded. Retained bycatch represented ca. 4% of the total catch by weight (Fig. 4b).

Table 2. Catch composition in seabob shrimp fisheries off Suriname based on 68 catch samples. For each catch fraction, including shrimp and different bycatch fractions, the average (±SD) catch-per-unit-effort (CPUE) and relative catch portion (by weight) are given. Further, average bycatch-to-shrimp ratios are presented.

	Shrimp	Bycatch			
		Total Bycatch	Fish	Jellyfish	Benthos
CPUE (kg/h)	113.4 ± 74.6	91.5 ± 119.9	72.1 ± 114.4	16.7 ± 23.5	2.7 ± 6.0
Relative portion (%)	59.1 ± 13.3	40.9 ± 13.3	31.2 ± 13.5	8.0 ± 9.8	1.7 ± 3.4
Bycatch ratios		bycatch:shrimp	fish:shrimp	jellyfish:shrimp	benthos:shrimp
		0.81 ± 0.58	0.61 ± 0.45	0.17 ± 0.28	0.03 ± 0.07

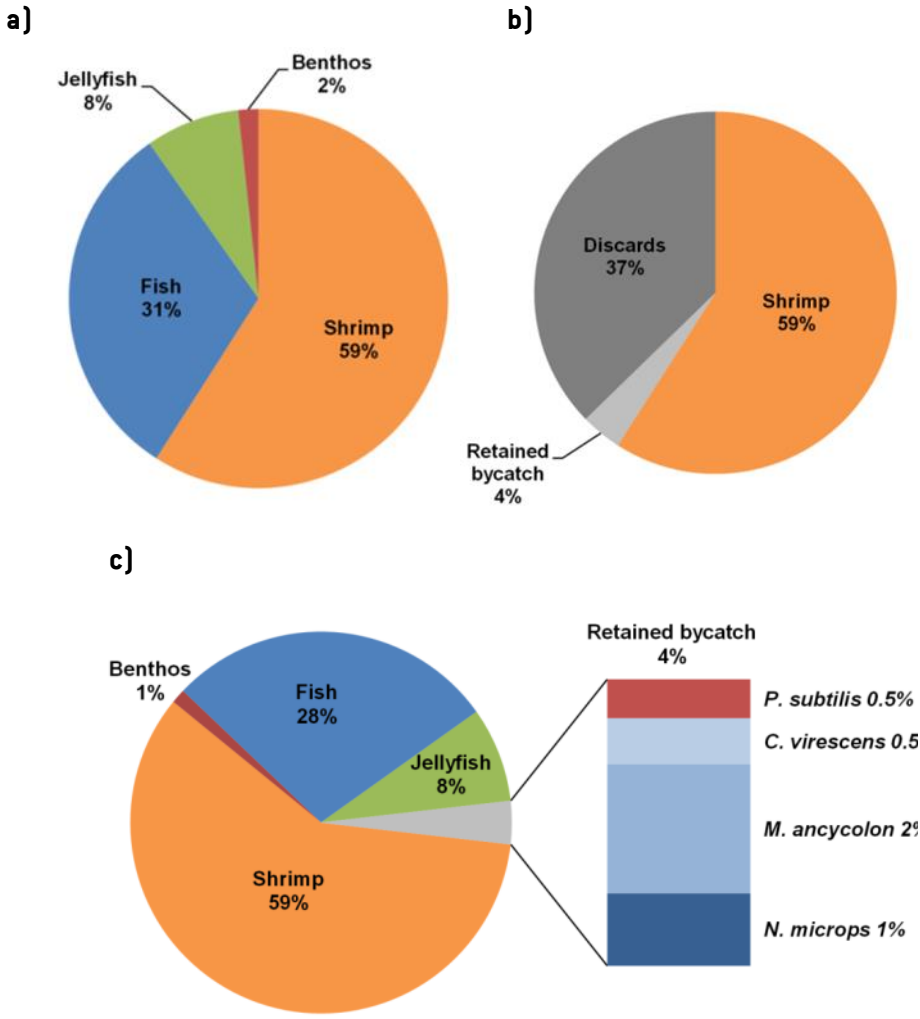

Figure 4. Average relative portions (by weight) of target catch (shrimp), bycatch (fish, jellyfish and benthos) and retained bycatch in the seabob shrimp fishery off Suriname. Shrimp is mainly seabob shrimp *Xiphopenaeus kroyeri*, but might also include small amounts of whitebelly shrimp *Nematopalaemon schmitti*. a) proportions of shrimp and the three bycatch fractions, b) proportions of shrimp and retained versus discarded bycatch, c) idem to b), but with information on the compostion of retained and discarded bycatch.

3.1.2 FISH BYCATCH

Fifty-four species of fish were identified in the bycatch. Twenty-two of these were rather rare, i.e. occurring in less than 5% of the samples (Table 3). Fish bycatch was largely dominated by two Sciaenid fishes, *Stellifer microps* and *Cynoscion jamaicensis*, accounting for 50% of fish bycatch by weight and both species occurred in 100% of the samples. While the remaining 50% included a diverse array of species, Sciaenidae was the major fish family here as well (Fig. 5).

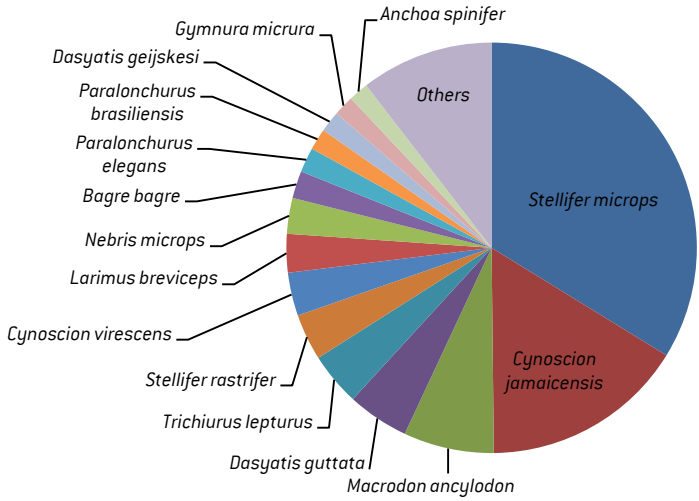

Figure 5. Average relative portions (by weight) of fish bycatch species in the seabob shrimp fishery off Suriname. 'Others' includes 39 species with low relative contributions.

Most fishes were small, measuring under 20 cm total length. The five most common bycatch species (based on %FO; Table 3), *C. jamaicensis, S. microps, A. spinifer, S. rastrifer* and *S. plagiusa* mostly measured around 10 cm total length. Further, the commercially valuable species *M. ancylodon*, *C. virescens* and *N. microps* had peak length-distributions below 25 cm, the average size at which they are retained (Fig.6). Retained fish bycatch, calculated as the combined weight of fishes of these three species measuring >25 cm, accounted for 10.1 ± 11.1 % of the fish fraction (by weight). *Macrodon ancylodon* was the most important retained species (5. ± 3 7.5 % of the fish fraction), followed by *C. virescens* (1.9 ± 5.8 %) and *N. microps* (2.9 ± 5.3 %) (Fig. 4c).

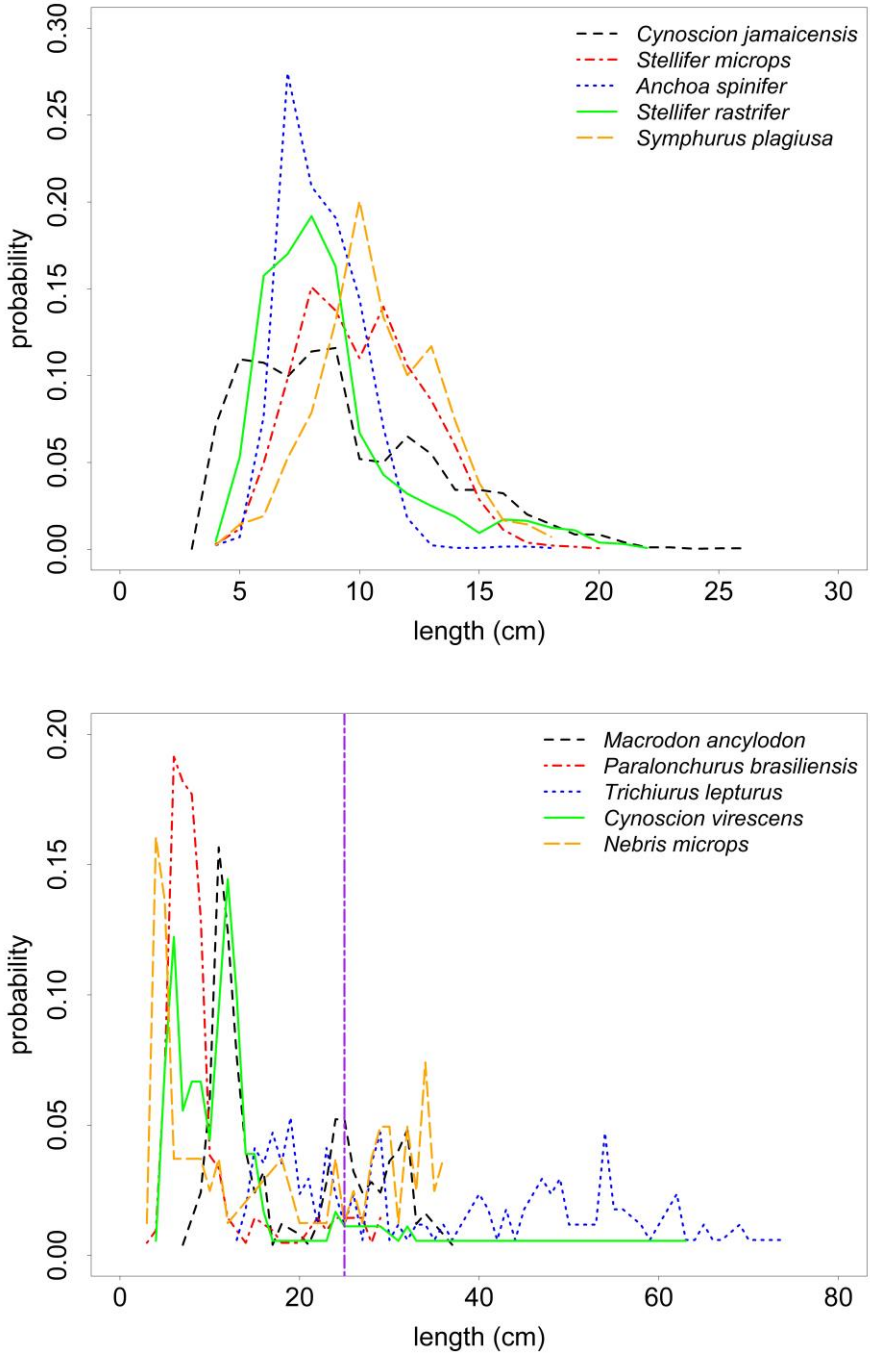

Figure 6. Length-distributions of the 10 most common fish bycatch species in the seabob shrimp fishery off Suriname. Length-frequencies were standardized by totals to yield a probability length-distribution. The purple line on the lower plot indicated the size (25 cm) at which the commercial species *M. ancylodon*, *C. virescens* and *N. microps* are usually retained.

Table 3. Fish bycatch species identified from 68 catch samples in the seabob shrimp fishery off Suriname. For each species the frequency of occurrence (%FO) and catch-per-unit-effort (CPUE) is given, both in terms of weight (kg/h) and numbers (#/h).

Order	Family	Species	%FO	CPUE (kg/h)	CPUE (#/h)
Anguilliformes					
	Muraenesocidae	*Cynoponticus savanna*	7.4	0.6 ± 3.1	1.0 ± 4.1
	Muraenidae	*Gymnothorax ocellatus*	1.5	<0.1 ± 0.2	0.2 ± 1.3
Aulopiformes					
	Synodontidae	*Saurida caribbaea*	2.9	<0.1 ± 0.0	0.2 ± 1.1
Batrachoidiformes					
	Batrachoididae	*Batrachoides surinamensis*	4.4	<0.1 ± 0.1	0.4 ± 2.1
Carcharhiniformes					
	Triakidae	*Mustelus higmani*	2.9	0.1 ± 0.4	0.2 ± 1.4
Clupeiformes					
	Clupeidae	*Harengula jaguana*	20.6	0.3 ± 1.1	6.6 ± 24.5
		Harengula sp.	1.5	<0.1 ± 0.0	0.1 ± 0.7
	Engraulidae	*Anchoa spinifer*	85.3	1.1 ± 1.5	374.5 ± 732.8
		Anchoviella lepidentostole	29.4	<0.1 ± 0.1	24.7 ± 85.1
	Pristigasteridae	*Odontognathus mucronatus*	36.8	0.1 ± 0.1	12.5 ± 27.4
Lophiiformes					
	Ogcocephalidae	*Ogcocephalus sp.*	1.5	<0.1 ± 0.0	0.3 ± 2.5
Perciformes					
	Carangidae	*Caranx hippos*	2.9	0.9 ± 7.0	0.3 ± 2.0
		Selene brownii	4.4	<0.1 ± 0.1	0.9 ± 5.7
		Selene vomer	7.4	0.2 ± 0.8	2.1 ± 10.5
	Centropomidae	*Centropomus ensiferus*	1.5	0.1 ± 1.1	0.2 ± 1.8
	Ephippidae	*Chaetodipterus faber*	5.9	<0.1 ± 0.0	0.6 ± 3.1
	Haemulidae	*Haemulon boschmae*	8.8	0.1 ± 0.5	1.5 ± 5.3
		Orthopristis ruber	8.8	0.2 ± 0.9	1.9 ± 7.4
	Polynemidae	*Polydactylus oligodon*	32.4	0.6 ± 1.6	7.0 ± 17.7
	Sciaenidae	*Ctenosciaena gracilicirrhus*	22.1	0.4 ± 1.3	20.5 ± 59.9
		Cynoscion jamaicensis	100.0	11.6 ± 31.6	822.8 ± 1477.0
		Cynoscion virescens	51.5	2.5 ± 7.0	28.7 ± 45.9
		Larimus breviceps	22.1	2.2 ± 12.4	20.1 ± 117.2
		Lonchurus elegans	30.9	1.4 ± 2.9	11.6 ± 21.9
		Lonchurus lanceolatus	4.4	0.1 ± 0.8	2.3 ± 12.2
		Macrodon ancylodon	66.2	5.1 ± 9.3	47.6 ± 74.3
		Menticirrhus americanus	5.9	0.3 ± 1.1	0.9 ± 4.0
		Micropogonias furnieri	1.5	<0.1 ± 0.3	0.1 ± 1.2
		Nebris microps	51.5	2.0 ± 4.1	13.2 ± 18.5
		Paralonchurus brasiliensis	66.2	1.2 ± 4.6	43.1 ± 60.4
		Plagioscion auratus	30.9	0.3 ± 0.6	9.4 ± 19.7
		Stellifer microps	100.0	24.3 ± 33.5	1598.1 ± 1710.3
		Stellifer rastrifer	79.4	2.6 ± 4.4	229.7 ± 361.3
	Serranidae	*Diplectrum sp.*	1.5	<0.1 ± 0.0	0.1 ± 0.8
	Stromateidae	*Peprilus paru*	4.4	<0.1 ± 0.0	1.1 ± 5.6
	Trichiuridae	*Trichiurus lepturus*	58.8	3.0 ± 7.9	34.8 ± 75.9
Pleuronectiformes					
	Achiridae	*Achirus achirus*	33.8	0.3 ± 1.2	7.2 ± 18.4
	Cynoglossidae	*Symphurus plagiusa*	73.5	0.9 ± 1.5	70.7 ± 109.9
Rajiformes					
	Dasyatidae	*Dasyatis geijskesi*	2.9	1.2 ± 8.9	0.6 ± 3.4
		Dasyatis guttata	20.6	3.5 ± 11.8	4.3 ± 11.5
	Gymnuridae	*Gymnura micrura*	20.6	1.2 ± 9.4	5.4 ± 18.3
	Rhinobatidae	*Rhinobatos percellens*	4.4	0.5 ± 2.8	0.8 ± 4.0
	Urotrygonidae	*Urotrygon microphthalmum*	22.1	<0.1 ± 0.1	5.4 ± 14.4
Scorpaeniformes					
	Dactylopteridae	*Dactylopterus volitans*	1.5	<0.1 ± 0.0	0.2 ± 1.8
	Triglidae	*Prionotus punctatus*	7.4	<0.1 ± 0.1	0.6 ± 2.4
Siluriformes					
	Ariidae	*Amphiarius phrygiatus*	2.9	0.2 ± 1.4	0.4 ± 3.0
		Amphiarius rugispinis	22.1	0.4 ± 1.5	8.7 ± 34.5
		Aspistor quadriscutis	4.4	0.2 ± 1.1	0.5 ± 2.5
		Bagre bagre	20.6	1.6 ± 6.7	4.1 ± 13.0
		Notarius grandicassis	2.9	0.2 ± 1.7	1.2 ± 8.5
Tetraodontiformes					
	Diodontidae	*Chilomycterus antillarum*	1.5	<0.1 ± 0.3	0.5 ± 4.0
	Tetraodontidae	*Colomesus psittacus*	4.4	0.1 ± 0.7	0.8 ± 4.1
		Sphoeroides testudineus	1.5	<0.1 ± 0.1	0.2 ± 1.7
Torpediniformes					
	Narcinidae	*Narcine bancroftii*	13.2	0.2 ± 1.0	4.7 ± 25.2

3.1.3 BENTHOS BYCATCH

From the benthos bycatch, 24 benthic invertebrate taxa were identified (Table 4). Nine of these occurred in less than 5 % of all samples. The only commercially valuable and retained benthos species was Brown shrimp *P. subtilis*, representing 25% of the benthos bycatch by weight. The rest of benthos fraction was mainly made up of the crab species *C. ornatus, P. lichtensteinii* and *C. sulcata*, the gastropod *M. bufo*, the soft coral *R. muelleri* and the shrimp *E. oplophoroides* (Fig. 6).

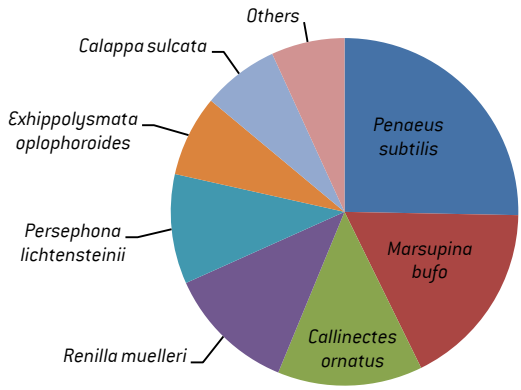

Figure 6. Average relative portions (by weight) of epibenthic invertebrate species (benthos) in the bycatch of the seabob shrimp fishery off Suriname. 'Others' includes 17 species with low relative contributions.

Table 4. Benthos (epibenthic invertebrate) species identified from 68 catch samples in the seabob shrimp fishery off Suriname. For each species the frequency of occurrence (%FO) and catch-per-unit-effort (CPUE) is given, both in terms of weight (kg/h) and numbers (#/h).

Higher rank	Species	%FO	CPUE (kg/h)	CPUE (#/h)
CRUSTACEA				
Decapoda - Penaeoidea				
	Penaeus subtilis	67.6	0.69 ± 1.26	49.8 ± 89.3
Decapoda - Anomura				
	Clibanarius foresti	8.8	0.02 ± 0.10	5.4 ± 25.4
	Dardanus fucosus	2.9	0.01 ± 0.03	0.5 ± 2.7
	Anomura sp.	5.9	<0.01 ± 0.01	0.8 ± 4.0
Decapoda - Brachyura				
	Acanthilia intermedia	1.5	<0.01 ± 0.01	0.4 ± 3.0
	Brachyura sp.	1.5	<0.01 ± 0.00	0.1 ± 1.2
	Calappa sulcata	33.8	0.19 ± 0.65	6.0 ± 9.8
	Callinectes ornatus	80.9	0.37 ± 1.09	243.8 ± 1193.2
	Hepatus gronovii	33.8	0.09 ± 0.18	9.0 ± 29.4
	Hepatus pudibundus	4.4	<0.01 ± 0.01	0.5 ± 2.3
	Paradasygyius tuberculatus	14.7	<0.01 ± 0.01	4.4 ± 19.7
	Persephona lichtensteinii	67.6	0.28 ± 1.08	222.5 ± 1194.3
	Portunus gibbesii	2.9	<0.01 ± 0.01	0.5 ± 2.9
	Raninidae sp.	7.4	<0.01 ± 0.00	0.7 ± 2.5
Decapoda - Caridea				
	Exhippolysmata oplophoroides	42.6	0.21 ± 1.20	223.4 ± 1207.6
Stomatopoda				
	Squilla sp.	48.5	0.04 ± 0.09	36.2 ± 98.1
MOLLUSCA				
Bivalvia				
	Bivalvia sp.	2.9	<0.01 ± 0.00	0.3 ± 1.8
Cephalopoda				
	Loligo sp.	8.8	<0.01 ± 0.01	1.3 ± 5.4
Gastropoda				
	Distorsio clathrata	1.5	<0.01 ± 0.01	0.1 ± 1.2
	Marsupina bufo	45.6	0.48 ± 1.12	47.8 ± 114.0
	Tonna galea	2.9	0.01 ± 0.06	0.1 ± 1.2
	Naticarius canrena	5.9	0.01 ± 0.02	0.7 ± 3.3
CNIDARIA				
Anthozoa				
	Renilla muelleri	32.4	0.33 ± 2.51	159.3 ± 1195.6
ANNELIDA				
	Polychaeta sp.	1.5	<0.01 ± 0.00	0.2 ± 1.8

3.2 TEMPORAL VARIABILITY IN THE BYCATCH

3.2.1 MONTHLY VARIABILITY

Both the overall CPUE (shrimp + bycatch) and the relative composition of the four catch fractions (shrimp, fish, jellyfish and benthos) differed significantly among months (Pseudo-F=5.6; P=0.0005 and Pseudo-F=8.4; P=0.0001, respectively). CPUE was highest in August, significantly higher than all other months except April. CPUE in April was significantly higher than in May and October (pairwise tests; $p<0.05$). Catch composition differed significantly among all months, except between May and August, and July and August (pairwise tests; $p<0.05$) (Fig. 7).

When taking into account all species of fish, benthos and jellyfish (the latter treated as one species), the bycatch community was significantly different among all months (Pseudo-F=5.8; P=0.0001) (pairwise tests; $p<0.05$). SIMPER revealed that these differences were mainly caused by slightly changing relative abundances (CPUE in terms weight) of the main bycatch species: *S. microps, C. jamaicensis, M. ancylodon, S. rastrifer, D. guttata, T. lepturus* and jellyfish.

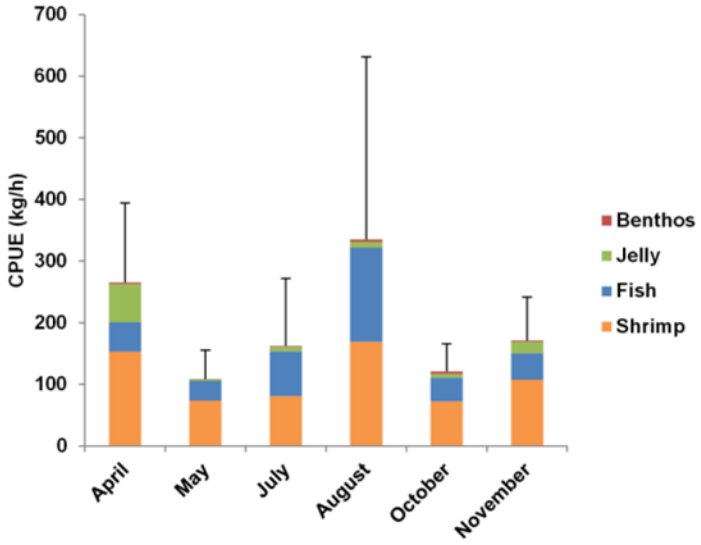

Figure 7. Catch-per-unit-effort (kg/h; +SD) in the seabob shrimp fishery off Suriname, represented for the 6 months (in 2014) when sampling took place.

3.2.2 DIURNAL VARIABILITY

While the average overall CPUE was lower during night time hauls (Fig. 8), this difference was not significant (P=0.1169). The relative catch composition of shrimp, fish, jellyfish and benthos did not differ between day and night either (P=0.9053), but the bycatch community (considering all species) did (Pseudo-F=2.5; P=0.0025). Species with the highest contribution to this difference were *S. microps, M. ancyldon, C. jamaicensis* and jellyfish, which all had a higher abundance during day time. Nevertheless, many species, mostly fishes, contributed to this day – night difference in the bycatch community (35 species to reach 90% of dissimilarity in SIMPER).

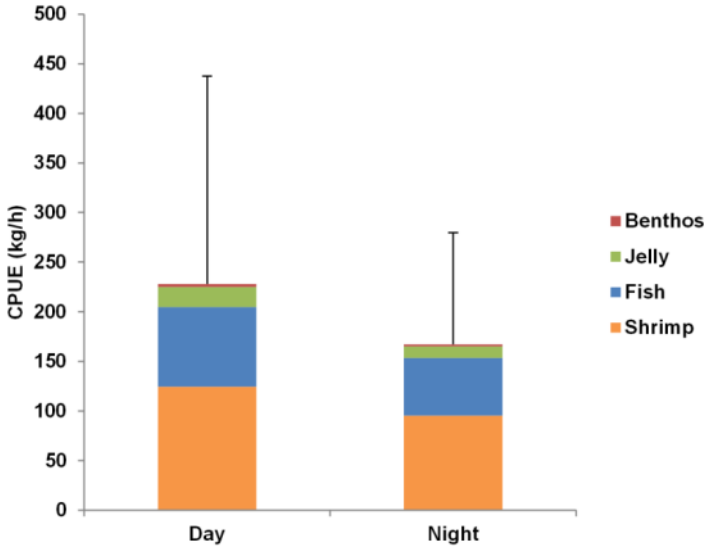

Figure 8. Catch-per-unit-effort (kg/h; +SD) in the seabob shrimp fishery off Suriname, averaged for hauls during daytime (7:00h-19:00h) and night time.

4 DISCUSSION

This study is the first to make a detailed assessment of the catch composition in the seabob shrimp trawl fishery off Suriname. Although we only sampled catches from a single vessel, all trawlers in the Suriname seabob fleet are similar, employ the same gear and work close to each other in the same area. As such, while we would have ideally included catch samples from different vessels, the data presented here are representative for the entire fishery.

We found an average bycatch:shrimp ratio of 0.81. In general, it is estimated that bycatch and shrimp are caught at ratios of 5:1 in temperate and subtropical regions, and 10:1 in the tropics (see Andrew and Pepperell, 1992 and references therein; EJF, 2003; Gillett, 2008). These ratios might be highly variable even within a fishery (Ye et al., 2000; Tonks et al., 2008), and considerable bias might be induced by different methods used to estimate bycatch-to-shrimp ratios (Ye, 2002; Diamond, 2003). Nevertheless, we can conclude that the Suriname seabob fishery is fairly selective for a tropical shrimp trawl fishery.

Because tropical shrimp trawling mainly targets Penaeid shrimp of the genus *Penaeus* (FAO, 1999), the high bycatch ratios that are typically reported, largely result from fisheries for *Penaeus sp.* Off the coast of Guyana, Suriname and French Guiana, an average bycatch:shrimp ratio as high as 40.2 has been reported in fisheries targeting *Penaeus brasiliensis, P. schmitti, P. notialis* and *P. subtilis* (Cummins and Jones, 1973 in Andrew and Pepperell, 1992). In contrast to the seabob shrimp *Xiphopenaeus kroyeri*, these species live further offshore, beyond the 30 m isobath on sandy bottoms (Guéguen, 2000a; Willems et al., 2015b). Off Suriname, *X. kroyeri* is known to reach densities up to ca. 1400 individuals m-2, while the maximum observed densities for *Penaeus sp.* was only 40 indiv. m-2 (Willems et al., 2015b). Assuming similar densities of bycatch species (either fish or benthos) in areas trawled for *Penaeus* sp. or *X. kroyeri*, the high densities in which *X. kroyeri* typically occurs, result in low bycatch levels, relative to fisheries targeting *Penaeus sp.* Low bycatch levels in *X. kroyeri* trawl fisheries were also observed in South-Eastern Brazil. Fish:shrimp ratios here averaged 0.57 (similar to our observed fish:shrimp ratio of 0.61), decreasing to 0.38 after the introduction of different types of BRDs (Cattani et al., 2012). In the same area, Silva et al. (2012) report that *X. kroyeri* on average constitutes 75% of the catch by numbers. It seems that, unlike other penaeid shrimp, *X. kroyeri* allows for a relatively selective fishery due to its high densities on the trawling grounds.

Despite this relative selectivity, 41% of the catch of the Suriname seabob fishery consists of bycatch, the majority of which is discarded (37% of the total catch). Southall et al. (2011), however, report that 31% of the catch is bycatch, about one-third of which is discarded. It is not immediately clear why our findings differ from these results, as CPUE of the seabob fleet has remained relatively constant over the years (Pérez, 2014), the gear has not changed, and practises

of discarding or retaining species doesn't seem to have changed either. (J. Jagroop, pers. comm.). Possibly, the overall biomass of the main bycatch species in the area has increased over the years, or the 2011-data were collected when these biomasses were low, due to seasonal effects.

Benthos only made up a small part (3% by weight) of the bycatch. This is consistent with the finding that the epibenthic community off Suriname up to ca. 30 m depth is species-poor, and largely dominated by the target species *X. kroyeri* (Willems et al., 2015b). In contrast, the area trawled for *X. kroyeri* is home to species-rich assemblages of demersal fishes, dominated by species of the Sciaenidae family (Willems et al., 2015a). Although these fish assemblages constitute of up to 61 species, they are characterized by a few abundant, and many rare species (Willems et al., 2015a), a pattern that is reflected in the bycatch of seabob fisheries. While 54 fish species were identified from the catch samples, only eight species made up 75% of the fish bycatch (by weight). Tropical shrimp trawl fisheries are known to catch a high diversity of bycatch species (Kelleher, 2005; Gillett, 2008). Still, the observation that a few species are numerically dominant seems a common feature of demersal fish assemblages on soft-bottom (sub-)tropical shelves (e.g. Rocha and Rossi-Wongtschowski, 1998; Chaves et al., 2003), and the bycatch composition of seabob trawl fisheries operating on these shelves (e.g. Bernardes Junior et al., 2011; Silva et al., 2012a; Branco et al., 2015).

On the inner Suriname shelf (up to 40 m depth), the demersal fish community changes drastically around the 30 m isobath, from an inshore sciaenid fish community on mud and sandy mud, to a deeper shelf community on offshore sandy bottoms (Willems et al., 2015a). Operating between 18 and 33 m depth, the seabob fishery overlaps with the *'coastal'* and '*transition'* demersal fish assemblages as described by Willems et al. (2015a). However, the relative composition of the most abundant bycatch species differed from the species composition of both assemblages (Fig. 9). The difference between these fish assemblages and the 'bycatch assemblage' could be assigned to the fact that the gear used to characterize these assemblages (try-net of 4.3 m horizontal spread; Willems et al., 2015a) differs from the commercial seabob trawls, which have a much larger horizontal (ca. 21 m) and vertical opening (ca. 2 m; B. Verschueren, pers. comm.). Further, in contrast to the try-net, these trawls are equipped with TEDs and BRDs, affecting the catch composition (e.g. Polet et al., 2010; Willems et al., 2016). On the other hand, seabob trawl fisheries do not operate randomly, but actively seek for high densities of seabob shrimp (Pérez, 2014). These 'hot spots' are known to be ephemeral, changing quickly in space and time (S. Hall, pers. comm.). Most likely, a typical 'assemblage' of demersal fishes is associated with these shifting patches of high shrimp densities. This is the 'bycatch assemblage' as observed in the current study, largely dominated by the sciaenids *S. microps* and *C. jamaicensis*. Their association with high *X. kroyeri* densities is not immediately obvious, as both species had rather low

contributions of this shrimp (around 15% gravimetrical contribution) to their diet (Willems et al. submitted b).

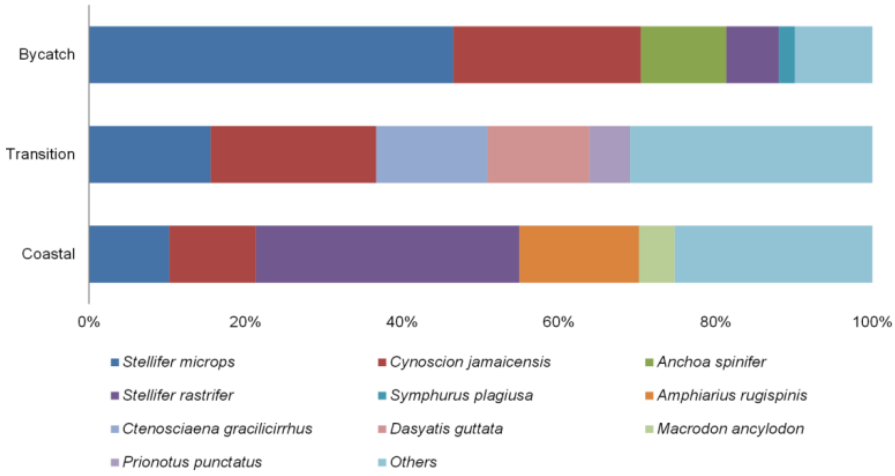

Figure 9. Relative catch composition (by numbers) of the top five most abundant fish species (by numbers) in the bycatch of seabob fisheries (top), the 'transition assemblage' (middle) and 'coastal assemblage' (bottom) of demersal fishes off Suriname (see Willems et al., 2015a).

Several fish species in the bycatch of seabob fisheries off Suriname are of commercial interest for the artisanal fishing fleet off Suriname. These include mainly *C. jamaicensis, C. virescens, M. ancylodon* and *N. microps,* which are targeted by gillnetting in the coastal waters up to 18 m depth (Bhagwandin, 2012; LVV, 2013). While individuals of the latter three species (>25 cm) are generally retained in the seabob fishery, their catches were dominated by small-sized, discarded specimens. Likewise, only small individuals of the dominant species *C. jamaicensis* were caught, which were all discarded. Due to trauma and injury induced by the catch process and handling on deck (e.g. Gillett, 2008), it is reasonable to assume that all rejected small teleost fishes are dead when discarded. Furthermore, discarded fish is consumed by scavenging seabirds (notably Common Terns *Sterna hirundo*, Cayenne Terns *Sterna eurygnatha* and Magnificent Frigatbirds *Fregata magnificens*; Willems et al. In Prep.) and predatory fishes (mainly Crevalle jack *Caranx hippos* and Cobia *Rachycentron canadum*) that follow the seabob trawlers (pers. obervation). As such, the mortality of bycaught and discarded commercial fishes might have a socio-economic impact, negatively affecting the artisanal fleet that targets these species.

Bycatch might also particularly affect species with a low natural resistance to fishing mortality, such as elasmobranchs (e.g. Stevens et al., 2000). Several ray species which are globally endangered and listed on the IUCN Red List of Threatened Species occurred in the bycatch, including *Dasyatis geijskesi* and *Rhinoptera bonasus* ('near threatened'), *Dasyatis guttata* and *Gymnura micrura*

('data deficient'), and *Urotroygon microphthalmum* ('least concern') (IUCN, 2015). While the use of TEDs has proven to significantly reduce their capture (Willems et al., 2016), our results show that all these species are still regularly caught, along with the electric ray *Narcine bancroftii* ('critically endangered') (IUCN, 2015).

Despite the use of BRDs and TEDs in the Suriname seabob fishery, fish bycatch still constitutes nearly one third of the total catch by weight. However, while the numbers of discarded commercial or vulnerable fish species are substantial, they tell little on the actual socio-economic or ecological consequences of bycatch mortality induced by the seabob fleet. Although the main teleost bycatch species in the Suriname seabob fishery are likely to be 'within biologically based limits' (Southall et al., 2011), no population estimates are available for any of these species. Due to the lack of stock assessments or mass-balance models (e.g. Ecopath with Ecosim; Christensen and Pauly, 2004), it is currently impossible to quantify the ecological and socio-economic effects of discarding. Therefore, a precautionary approach to bycatch management is recommended, which implies that bycatch should further be reduced, in the absence of models to define safe limits of bycatch mortality.

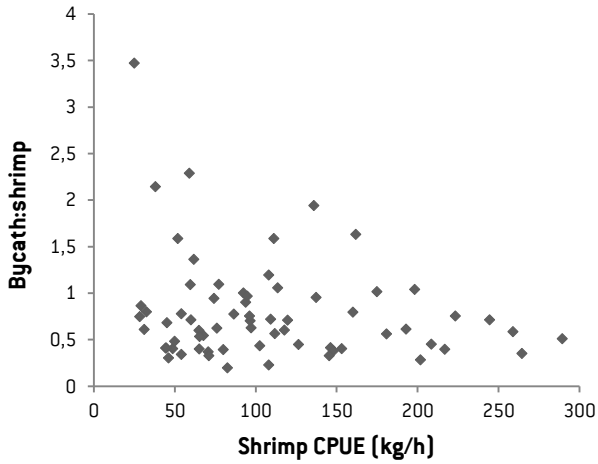

Figure 10. Scatterplot of shrimp catch-per-unit-effort (CPUE) and bycatch:shrimp ratios from 68 hauls in seabob shrimp fisheries off Suriname.

Bycatch reduction could be achieved through changes in the operational characteristics of the fleet. Through the use of a trynet and constant communication on shrimp catches among boats, the seabob trawling fleet off Suriname operates in a way that maximizes shrimp CPUE (Pérez, 2014). From our results, it seems that high bycatch:shrimp ratios are mainly associated with low shrimp CPUE (Fig. 10). As such, maximizing shrimp CPUE might effectively reduce bycatch ratios. This could be formalized in a 'move-on rule' (e.g. Auster

et al., 2011), requiring trawlers to change locations in case of excessive bycatch ratios. In Suriname's neighboring country Guyana, seabob trawl fisheries close each year for about 6 weeks in August – September, due to low shrimp CPUEs in these months (J. Jagroop, pers. comm). Conversely, we observed one of the highest shrimp CPUEs in August. Nevertheless, due to considerable short-term variability in shrimp CPUE (S. Hall, pers. comm.), more data should be analyzed to reveal real temporal patterns in catch characteristics that could serve as a basis for decisions on a temporal closure of the fishery in Suriname.

Bycatch reduction could also be accomplished by additional technical gear adaptations. In this respect, we would recommend trials with Nordmøre-grids. These have proven effective in reducing bycatch, while maintaining shrimp catches (e.g. He and Balzano, 2012), also in Brazilian seabob shrimp fisheries (Silva et al., 2012a). While efforts to reduce bycatch will affect the landings of commercially valuable bycatch, retained bycatch only accounted for 4% of the total catch by weight. Additional benefits of bycatch reduction might include reduction of fuel consumption due to reduced drag of codends through the water (Suuronen et al., 2012), and reduce the workload of catch sorting on deck.

ACKNOWLEDGEMENTS. *We thank captain Stephen Hall and crew from FV Neptune-6 for their support in data collection onboard. The Suriname Ministry of Agriculture, Livestock and Fisheries (LVV) and the Anton De Kom University of Suriname are acknowledged for supporting the research in various ways. We further thank the Heiploeg Group and Heiploeg Suriname N.V. for the financial and logistic support of the research. The first author acknowledges a PhD scholarship from VLIR-UOS (VLADOC2011–06).*

7

RAY BYCATCH IN A TROPICAL SHRIMP FISHERY: DO BYCATCH REDUCTION DEVICES AND TURTLE EXCLUDER DEVICES EFFECTIVELY EXCLUDE RAYS?

Modified from:

Willems,T., Depestele, J., De Backer, A., Hostens, K. 2016. Ray bycatch in a tropical shrimp fishery: Do Bycatch Reduction Devices and Turtle Excluder Devices effectively exclude rays? Fisheries Research 175, 35-42.

Worldwide, many species of elasmobranchs (Chondrichthyes: Elasmobranchii) are currently threatened by marine fisheries activity and are on the Red List of the International Union for Conservation of Nature (IUCN). Although Bycatch Reduction Devices (BRDs) for teleost fish and Turtle Excluder Devices (TEDs) are now widespread in tropical shrimp trawling, information on their ability to mitigate bycatch of elasmobranchs, particularly rays (Batoidea), is scarce and limited to only a few isolated fisheries. The objective of this study was to evaluate the potential of trawls fitted with a square-mesh panel BRD and super-shooter TED in reducing ray bycatch. In this study, 65 catch-comparison hauls were conducted in the Atlantic seabob shrimp (Xiphopenaeus kroyeri*) fishery off Suriname. Trawls with a BRD and TED combination reduced ray catch rate by 36%. A 21% reduction in mean size indicated the preferential exclusion of large rays. Hence, high escape ratios were observed for* Dasyatis geijskesi *(77%), a large-sized species, while exclusion of the small species* Urotrygon microphthalmum *was not significant, although their disc width is small enough to pass through the meshes of the BRD. Furthermore, a size-dependent escape for the two most abundant mid-sized ray species* Dasyatis guttata *and* Gymnura micrura *was observed. Exclusion-at-size differed for both species, however, likely related to species-specific morphology or behaviour in response to the TED. This study shows that the combination of BRD and TED causes an important reduction in ray bycatch in seabob shrimp fisheries off Suriname. The great reduction in catch of large-sized rays is positive, but the mortality of juvenile rays is likely to have negative consequences for their populations. We therefore recommend gear-based and non-gear adaptations to further reduce the bycatch of small-sized rays.*

1 INTRODUCTION

Concern has been increasing recently regarding the capture and mortality of elasmobranchs in marine fisheries (Stevens et al., 2000). In contrast to most teleost fish, elasmobranchs are generally slow-growing and long-lived, with late attainment of sexual maturity, low fecundity and low natural mortality (e.g. Goodwin et al., 2002; Fisher et al., 2013). This K-selected life-history strategy makes them particularly vulnerable to exploitation in fisheries, implying that overfished populations have a low ability to recover (Graham et al., 2001). Several species of elasmobranchs have been decimated and even brought to the brink of local extinction due to fishing activity (Dulvy et al., 2000; Dulvy and Reynolds, 2002; Baum et al., 2003). Elasmobranchs are also often of low economic value in fisheries that target teleost fish or invertebrates, and are hence discarded as unwanted bycatch (Stevens et al., 2000). Furthermore, elasmobranch discards often remain unreported (Worm et al., 2013), resulting in insufficient information on their occurrence and population sizes worldwide. This is a major impediment for effective conservation measures (Bonfil, 1994; Stevens et al., 2000).

Many species of elasmobranchs are known to occur as bycatch in tropical shrimp trawling (Simpfendorfer, 2000; Shepherd and Myers, 2005). Nonetheless, efforts to reduce bycatch in shrimp trawls have so far focused mainly on teleost fish and sea turtles through the development of Bycatch Reduction Devices (BRDs) and Turtle Excluder Devices (TEDs) (Broadhurst, 2000). Several types of BRDs have proven to cause significant reductions in the bycatch of non-commercial teleost fish (e.g. Rulifson et al., 1992; Rogers et al., 1997; Broadhurst, 2000; Heales et al., 2008). TEDs, on the other hand, are highly effective in reducing sea turtle bycatch (Robins and McGilvray, 1999; Eayrs, 2007; Eayrs, 2012). Moreover, they act as sorting grids, and exclude any organism larger than the TED's bar spacing (typically 10 cm) from the trawl, including large-sized elasmobranchs (Brewer et al., 1998; Griffiths et al., 2006; Brewer et al., 2006).

In the Atlantic seabob shrimp (*Xiphopenaeus kroyeri)* fishery off Suriname, trawls are required by law to be equipped with two widely-used devices: square-mesh panel BRD and super-shooter TED. In this fishery, these trawl adaptations have proven effective in reducing bycatch of non-target teleost fish (Polet et al., 2010) and sea turtles (S. Hall, pers. comm.), respectively. Average bycatch levels have now been reduced to ca. 40 % of the total catch by weight (Chapter 6), and most bycatch species in this fishery are assumed to be within safe biological limits (Polet et al., 2010; Southall et al., 2011; Southall et al., 2016). These efforts have contributed to the certification of the Suriname seabob shrimp fishery by the Marine Stewardship Council (MSC) in 2011. Nevertheless, the MSC assessment team raised particular concerns over mortality of rays (Elasmobrachii: Batoidea), which were identified as the most

vulnerable bycatch species. Ray bycatch remains a key issue to be tackled by the fishery in order to pass future MSC reassessments (Southall et al., 2011).

The Suriname seabob shrimp fishery is known to capture several ray species which are globally endangered and are listed on the IUCN Red List of Threatened Species, including *Dasyatis geijskesi* and *Rhinoptera bonasus* ('near threatened'), *Dasyatis guttata* and *Gymnura micrura* ('data deficient') (IUCN, 2015). Because these species commonly grow to 80 to 100 cm disc width (Léopold, 2005), we could expect them to escape through the TED. A fifth frequently caught ray species, *Urotrygon microphthalmum* ('least concern'; IUCN, 2015) is much smaller with a maximum disc width of 25 cm (Léopold, 2005), and might escape through the square-mesh panel BRD because of its small size. On the other hand, due to their flattened body shape and high flexibility, even large rays might still be able to pass between the bars of a TED and end up in the codend. With the exception of very small rays, their size and morphology would also prevent escape through the BRD. It remains unclear how frequently these rays occur in the bycatch of this fishery, and to what degree the current trawl adaptations (i.e. BRD and TED) reduce their capture.

In the present study, we have assessed the effectiveness of the combination of BRD and TED in reducing bycatch of rays in the Atlantic seabob shrimp fishery off the coast of Suriname. We present the results of a catch-comparison study in which we have focused on ray bycatch and analysed ray catches in trawls with and without the combination of BRD and TED. The aims were to assess whether these devices are effective in excluding rays from the trawls, and whether exclusion of rays is species- and size-dependent.

2 MATERIALS AND METHODS

2.1 STUDY AREA

The study was conducted on commercial fishing grounds for seabob shrimp (6.17°N to 6.25°N and 55.39°W to 55.84°W) on the continental shelf off Suriname (FAO Statistical area 31). This area is characterized by mud and sandy mud substrates and water depth is typically 20-25m (Fig. 1). Commercial shrimp fishing activity occurs year-round in this area.

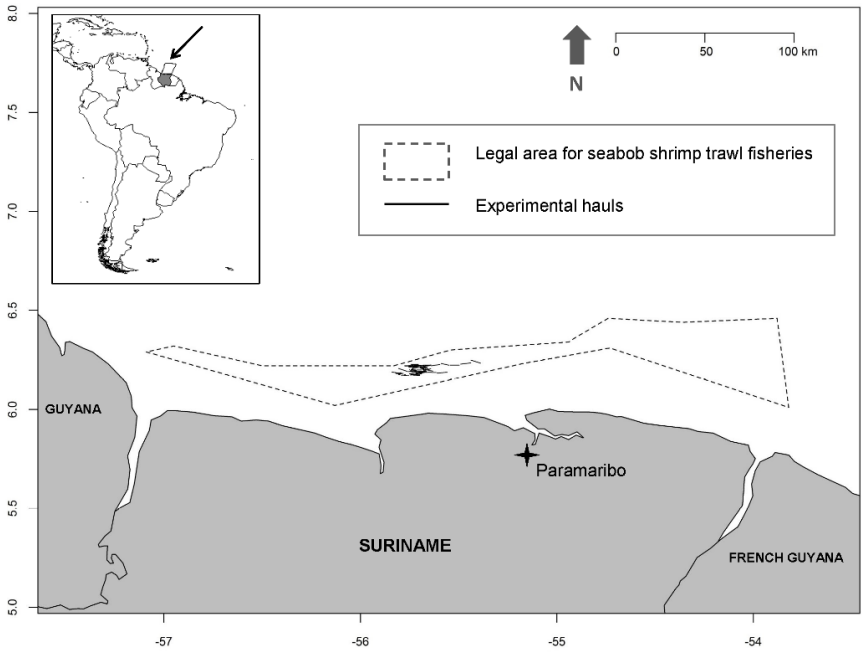

Figure 1. Study area with location of the experimental hauls.

2.2 GEAR SPECIFICATIONS

Hauls were done onboard FV *Neptune-6*, a typical 20-m, 425-hp 'Florida-type' outrigger trawler used in the seabob shrimp trawling fleet. The vessel was equipped for quad-rig bottom-trawling, which involves dragging two trawls attached to two steel-footed wooden doors and a sledge at either side of the vessel, resulting in two port- and two starboard-codends. Mesh size of each trawl was 57 mm in the body and wings of the trawl and 45 mm in the codend. Each trawl was fitted with an aluminum super-shooter TED. Bar spacing was 10 cm and each was installed in a downward-excluding configuration in an angle

of approximately 50° from the horizontal. A single net flap covered each bottom escape opening, and there was no guiding funnel in front of the TED. Each trawl was also fitted with a square-mesh-panel (11 x 11 meshes, 15 cm stretched mesh size) BRD inserted ca. 40 cm behind the TED in the upper side of the codend (Fig. 2).

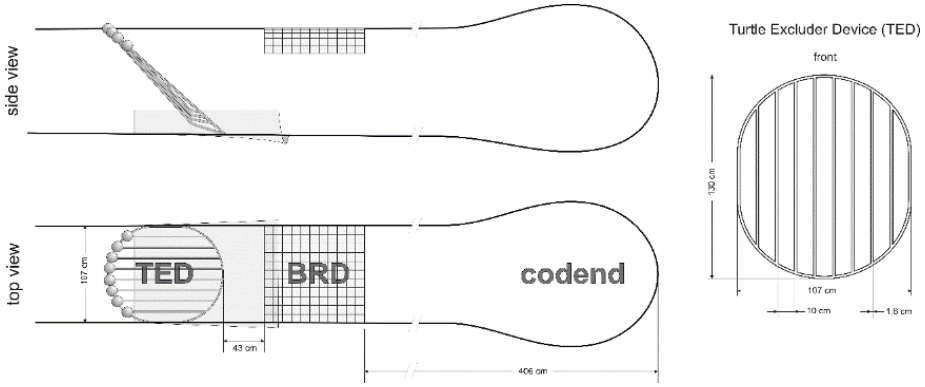

Figure 2. Sketch of a wBT trawl codend fitted with Bycatch Reduction Device (BRD) and super-shooter TED.

2.3 SEA TRIALS AND CATCH SAMPLING

A total of 65 experimental catch-comparison hauls were conducted on eight commercial seabob fishing trips between February 2012 and April 2013. During each trip, seven to ten experimental hauls were conducted to compare ray bycatch in trawls with a BRD and TED combination ('wBT net') versus trawls without a BRD and TED combination ('noBT net'). In the noBT net, both codends with BRD and TED were removed and replaced by codends without any devices. The side of the vessel dragging the wBT and noBT net was alternated every trip to exclude port and starboard effects. Hauls were done under commercial fishing circumstances, except for a shortened dragging time (avg. 1h16' ± SD 0h16' versus 3-4h normal dragging time), to reduce the risk of injury or mortality of vulnerable species in the noBT net. Although the fishery normally operates day and night, experimental hauls were done during daytime only for practical reasons. The wBT net and noBT net were dragged alongside each other at a speed of 2.5 to 3.5 knots, in accordance with normal fishing practice (Pérez, 2014). To ensure that the catches from the wBT and noBT nets remained separate, the two wBT codends were unloaded separately from the two noBT codends on deck. Per net, the catch from the two codends was combined. All rays were sorted out from the catches, identified to species level and measured (disc width) to the nearest centimeter. The catch was subsequently processed as usual by the crew and could not be analysed further for practical reasons.

2.4 DATA ANALYSIS

Ray catches were recalculated to a standardized catch rate (individuals h^{-1}). Differences in mean catch rate between the wBT and noBT net were analysed using Wilcoxon signed rank tests. Differences in mean ray size between wBT and noBT net were analysed with Mann-Whitney U tests. Both analyses were done per ray species and for all rays combined.

Differences in mean size among ray species were tested using the Kruskal-Wallis test and Nemenyi-post-hoc pairwise comparisons (Pholert, 2014). For these analyses, only data from noBT net catches were used because size-selection was expected in the wBT net. Non-parametric tests were used because the assumptions for (paired) t-tests and ANOVA were not met.

The relationship between ray size and escape from the trawls was explored using Generalized Linear Mixed Models (GLMM). To do so, size classes (originally 1 cm) were lumped and/or hauls with sufficient individuals per size class were selected to obtain enough data-points per size class. The proportion retained by the wBT net at size class S can be expressed for each size class and each haul as:

$$\varphi(S) = N_{S,wBT}/(N_{S,wBT} + N_{S,noBT})$$

where $\varphi(S)$ is the probability of catching an individual at size class S in the wBT net. $N_{S,wBT}$ and $N_{S,noBT}$ are the number of rays at size class S measured for the wBT net (with a BRD and TED combination in both trawls) and the noBT net (without BRDs and TEDs), respectively. A value of $\varphi = 0.5$ indicates that there are no differences in catch in numbers between the two nets at size class S. The catch-at-size proportion $\varphi(S)$ was modelled using the GLMM with binomial distribution and logit link function, according to the method described by Holst and Revill (2009). The expected proportion of the catch retained by the wBT net at size class S was expressed as:

$$\text{logit}[\varphi(S)] = \beta_0 + \beta_1 S_1 + \beta_2 {S_2}^2$$

where β_0 is the intercept coefficient, β_1 and β_2 the model coefficients for respectively the linear and quadratic effects of the explanatory variable 'size class S'. The catch comparison curves vary among hauls, potentially in a size-specific manner. In addition to the fixed effects, inter-haul correlation was incorporated into the models by the inclusion of random intercept and/or slope effects (Venables and Dichmont, 2004).

Escape-at-size was modelled for all ray species combined and for species frequently caught, i.e. present in ≥ 20 hauls with a minimum of 20 individuals. This was the case for *Dasyatis guttata* and *Gymnura micrura*. Size classes of 10 cm were used to make a model of all ray species combined over a large size

range (20 - 90 cm). For *D. guttata* and *G. micrura* a finer resolution (3-cm size classes) were used in a more restricted size range based on 24 and 25 hauls with > 20 individuals per haul, respectively. The *D. guttata* model was fitted between 20 and 72 cm and the *G. micrura* model between 18 and 57 cm. All analyses were carried out using R statistical environment (R Core Team, 2013).

3 RESULTS

Rays were caught in every experimental haul performed. A total of 3181 individuals were captured, comprising of five different species. Smooth butterfly ray (*Gymnura micrura*) and Longnose stingray (*Dasyatis guttata*) were the most abundant species, contributing 45% and 37% to the total ray catch by number, respectively. Smalleyed round stingray (*Urotrygon microphthalmum;* 11%), Sharpsnout stingray (*Dasyatis geijskesi;* 6%) and Cownose ray (*Rhinoptera bonasus;* 1%) were less abundant (Fig. 3). Mean catch rate of rays in the noBT net ranged from 6.3 ± 3.1 to 45 ± 19.6 ind. h-1 (average ± SD of May resp. April 2012) corresponding to a mean density of 0.6 ± 0.3 to 4.3 ± 1.9 rays ha-1 trawled in the study area.

Overall, mean catch rate of rays (over all hauls) was significantly reduced by 36.1% in the wBT net (15.3 ± 13.2 ind. h-1) compared to the noBT net (23.9 ± 19.2 ind. h-1; $p<0.001$). Significant reduction in catch rate in the wBT net was observed for *D. geijskesi* (-76.6%), *D. guttata* (-40.2%) and *G. micrura* (-32.1%; all $p<0.001$). Catch rate reductions in *R. bonasus* and *U. microphthalmum* were not significant (Fig. 3).

Size of rays captured during the experiment ranged from 3 to 116 cm with a mean of 29.6 ± 16.8 cm. Mean sizes of rays caught in the noBT net were statistically different among species ($\chi^2(4)=737.2$; $p<0.001$). Post-hoc tests revealed that all species differed significantly in mean size ($p<0.001$) except for *R. bonasus*, which did not differ from any other species (Fig. 4). Rays caught in the wBT net (avg. 25.5 ± 12.4 cm) were on average 20.6% smaller than rays caught in the noBT net (avg. 32.2 ± 18.6 cm; $p<0.001$). Size reduction in the wBT net was significant for *D. geijskesi* (37.8%; $p<0.001$) and *D. guttata* (22.7%; $p<0.001$) (Fig. 4).

The modelled proportion of rays retained by the wBT net was always <0.5, indicating an overall exclusion from the wBT net. Furthermore, the proportion-at-size of rays caught in the wBT net was size- and species-dependent (Fig. 5). Catch rate of all species combined declined with increasing size, following a quadratic curve in the modelled size-range. Total exclusion from the wBT net was approached at 90 cm disc width (Fig. 5; Table 1). A similar response was found for *D. guttata*, although the curve was steeper, reaching total exclusion

near 50 cm. Catch rate reduction for *G. micrura* was linear and did not approach zero in the modelled size-range (Fig. 5; Table 1).

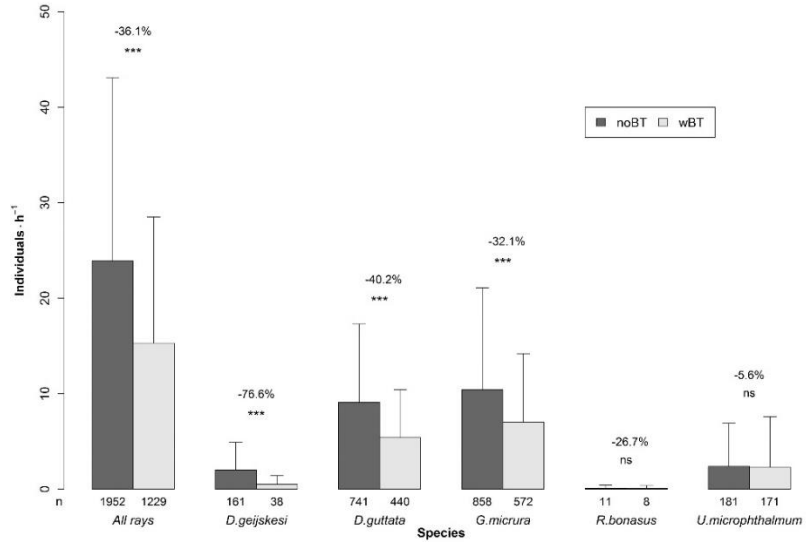

Figure 3. Mean (+SD) catch rate of rays in noBT net (dark grey) and wBT net (light grey). Percentages denote reduction in mean catch rate in the wBT net. Asterisks indicate significant differences (Wilcoxon signed rank tests; *** = P<0.001; ns = not significant); n = number of individuals.

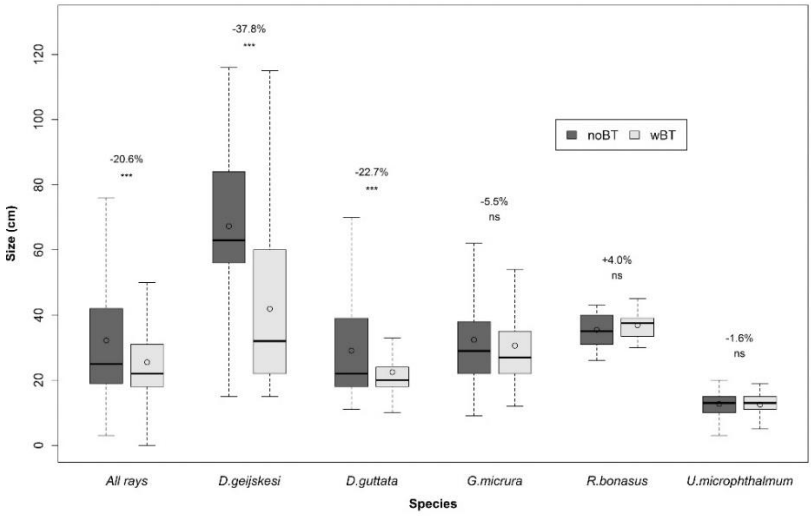

Figure 4. Box-and-whisker-plots showing minimum, maximum, 0.25 percentile, 0.75 percentile and median size (disc width) of the different ray species in noBT net (dark grey) and wBT net (light grey). Open circles indicate the mean size and percentages denote reduction in mean size in the wBT net. Asterisks indicate significant reductions (Mann-Whitney U tests; *** = P<0.001; ns = not significant).

Table 1. Coefficient values and significance (P-value) from generalised linear mixed modelling (GLMM) of the proportion (φ) of the catch excluded by the wBT net in relation to size (S), where logit[φ(S)] = $\beta_0 + \beta_1 S + \beta_2 S^2$. β_0 = intercept, β_1 = size, β_2 = size^2.

Species	Parameter	Estimate	SE	P-value
All ray species	β_2	-0.0006	0.0001	<0.001
Dasyatis guttata	β_1	0.0700	0.0261	0.0073
	β_2	-0.0035	0.0012	0.0022
Gymnura micrura	β_1	-0.0145	0.0057	0.0104

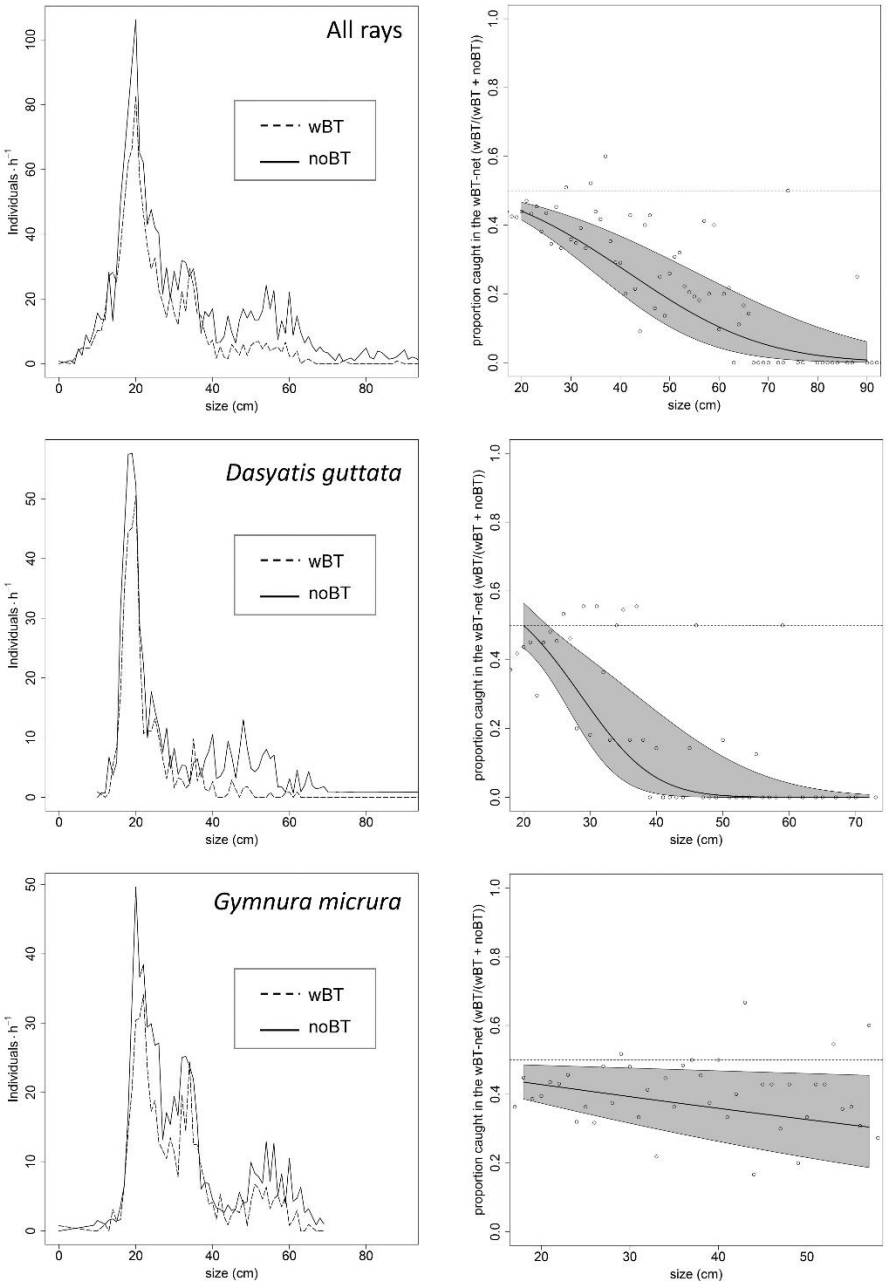

Figure 5. Size distribution and GLMM of size for all ray species combined and for *Dasyatis guttata* and *Gymnura micrura*. Left-hand plots present size-frequency distributions in wBT net (dashed) and noBT net (solid). Right-hand plots present the GLMM modelled proportion (shaded area = 95% CI) of the total catch in the wBT net. Interpretation: a value of 0.5 (dashed line) indicates an even split between the two trawls, whereas a value of 0.2 indicates that 20% of all rays at that size were caught in the wBT net and 80% were caught in the noBT net.

4 DISCUSSION

The combined use of BRD and TED in the Suriname seabob shrimp fishery caused a significant 36.1% reduction in the overall catch rate of rays. In one of the few other studies that quantified the effect of BRDs and TEDs on ray catch rate (Brewer et a*l.* 2006), a remarkably similar 36.3% reduction in Australia's northern prawn trawl fishery was found. This reduction was assigned to the effect of the TED, as no significant reduction in ray bycatch was found in trawls exclusively equipped with a BRD (bigeye or square-mesh panel). Although the effect of BRD and TED cannot be evaluated separately in the present study, the observed catch-rate reductions are likely to be caused by the TED rather than the BRD for the following reasons: No significant reduction was observed for *U. microphthalmum,* the only species which could theoretically escape through the meshes of the BRD due to its small size. Moreover, rays caught in the trawls with a BRD and TED combination were on average 20.6% smaller than those in the trawls without devices, indicating a tendency for larger rays to escape. If small-sized rays would be escaping from the trawl through the BRD, this would theoretically cause a relative size increase instead of the observed decrease.

We further quantified the effect of body size on escape ratio and confirmed that escape was size-dependent, with high escape ratios (>80%) for large individuals (>50cm). Still, factors other than size may affect escape ratio as well. Exclusion-at-size was clearly different between the two modelled species *D. guttata* and *G. micrura.* Looking at their morphology, *D. guttata* has a thick and rigid disc, in contrast to the more flexible and smooth body of *G. micrura*. *Gymnura micrura* might more easily bend and slip in between the bars of the TED, while a similar-sized individual of *D. guttata* is more likely to escape upon interaction with the TED. A TED is classified as a mechanical excluder, separating species according to size and morphology rather than behaviour (Broadhurst, 2000). Nevertheless, behavioural differences between species are known to influence escape from trawls (e.g. Hannah and Jones, 2012) and could be of importance here also.

Fish escaping from trawls may suffer delayed mortality due to injury or stress caused by the catch-and escape-process (Suuronen, 2005). The survival of rays escaping the trawls through the TED remains unclear. Likewise, although discarded rays might have higher chances of survival than teleost fish (Depestele et al., 2014), the fate of rays that are brought on deck and subsequently discarded is not well understood.

The performance of BRD and TED was assumed constant during the study. Even though the gear was inspected before each trip, including monitoring of the grid angle, wear and damage of the gear might well have affected BRD and TED performance (e.g. Eayrs S., 2007), and hence exclusion of rays.

Nevertheless, our results reflect the conditions encountered over a long period of time, under normal commercial fishing conditions.

A very high escape ratio (77%) was observed for *D. geijskesi,* linked to the fact that most individuals of this species were rather large. Escape ratios for *D. guttata* (40%) and *G. micrura* (32%) were lower. In both species, the dominant catches were small-sized individuals that were unable to escape from the trawls. Nevertheless, the models for both species showed that larger specimens did escape efficiently from the trawls equipped with a BRD and TED combination. Because fecundity tends to increase with body size, the protection of large-sized individuals is essential to maintain productive populations (Stevens et *al.*, 2000). Furthermore, recruitment of cartilaginous fishes to the adult population is very closely linked to the number of breeding females (Taylor et al., 2013).

Females of *D. guttata* are mature from 50-55 cm onwards (Yokota and Lessa, 2007). Our results show a nearly complete exclusion from the trawls at this size, allowing for potential survival of breeding females. Still, as has been shown for *Dasyatis dipterura* in the Gulf of Mexico, survival of both adult and juvenile stages strongly influences population growth rates (Smith et al., 2008). For *G. micrura*, first maturity of females occurs at 34-36 cm (Yokota and Lessa, 2007), a size at which exclusion from trawls with TEDs was low. Due to its relatively early maturity, the species could be more resilient than *D. guttata* (Walker and Hislop, 1998), and better able to cope with a reduced exclusion rate. Nevertheless, *G. micrura* appeared as a vulnerable elasmobranch species in the Gulf of Mexico, where it has undergone a 99% decrease since the early 1970s due to shrimp trawling (Shepherd and Myers, 2005). Both *D. guttata* and *G. micrura* are red-listed as 'data deficient' (Rosa and Furtado, 2004; Grubbs and Ha, 2006), and any population estimates for the study area are lacking.

No reduction in catch rate was observed for *U. microphthalmum*. Although the species is currently assessed as 'least concern' (Rosa, 2004), the TED caused no reduction in bycatch of this species because of its small size (max. 25 cm; Léopold, 2005) and it did not appear to escape through the BRD either. This species might therefore be prone to high fishing mortality in shrimp trawls. Insufficient data were collected to make any conclusions on *R. bonasus* from the current study ('near threatened'; Barker, 2006).

The current study shows that TEDs cause a significant reduction in the bycatch of rays, although reduction was highly dependent on size and species-specific morphology. Whilst larger rays were able to escape at a relatively high rate, rays with a disc width of approximately 20 cm were most common, a size at which escape ratio was lower (<60%). This is still a positive result, given that in the pre-TED days a much higher percentage of small rays would not survive. However, improvement in the escapement of small rays is required. Smaller

rays are less likely to survive the discard process than larger ones (Davis, 2002; Benoit et al., 2013; Depestele et al., 2014), adding to their effective mortality relative to larger rays. Although few direct estimates have been generated for elasmobranch fishes (e.g. Simpfendorfer, 1999; Gruber et al., 2001), their natural mortality is assumed to be low (Cailliet et al., 2005; Cortes, 2007). Any fisheries-induced mortality, even of juvenile rays, is thus likely to significantly affect the ray populations.

In conclusion, we have shown that the BRD and TED combination causes an important reduction in ray bycatch in the seabob shrimp fishery off Suriname. Despite the large reduction in catch rates of large-sized rays, the relatively high rate of mortality of juvenile rays is likely to have negative consequences for their populations. As very little information is currently available, a precautionary approach in fisheries management is advisable until assessments of the population sizes and status of the rays in these fishing grounds become available. Future gear adaptations and efforts should focus on reducing bycatch of small-sized rays. To our knowledge, no trawl modifications have been developed to specifically tackle ray bycatch; we therefore suggest an assessment of the ability of sorting grids with reduced bar spacing to exclude small-sized rays while still catching shrimp. Assessing the potential of super-shooter TEDs with smaller bar spacing seems to be a logical next step. Another option could be Nordmøre-grids, as they have shown not to affect shrimp catches in a Brazilian seabob shrimp fishery, even when the bars are spaced only 17 mm apart (Silva et al., 2012a). Finally, square-mesh panel BRDs with larger meshes to reduce small-sized rays could also be tested. Non gear-related solutions can include spatial and temporal restrictions to fishing effort, changes in fishing practices (e.g. move-on rules; Auster et al., 2011) and modifications in catch handling on deck to increase post-capture survival (Depestele et al., 2014; Enever et al., 2008).

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PART IV

TOWARDS SUSTAINABLE MANAGEMENT OF *XIPHOPENAEUS KROYERI* FISHERIES IN SURINAME


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GENERAL DISCUSSION: INTEGRATING SCIENTIFIC KNOWLEDGE AS A BASELINE FOR FISHERIES MANAGEMENT

The aim of this doctoral study was to provide relevant knowledge for the development of an improved ecosystem-based approach to the management of Xiphopenaeus kroyeri *trawl fisheries off Suriname. Structural and functional aspects of the ecosystem of the inner Suriname Shelf were studied, along with ecosystem impacts of fishing. The aim of this chapter is to translate the scientific findings into guidelines to implement an Ecosystem Approach to Fisheries (EAF). First, we present a theoretical framework on how to move from science to policy in an EAF. Next, we review the main scientific findings of this doctoral thesis, by answering questions related to the three mains aspects to be considered in an EAF. Based on the obtained results, the current management measures in the Suriname seabob fishery are evaluated and recommendations are made. Finally, we formulate considerations on the wider application of an EAF in Suriname, and define priorities for future research.*

1 FROM SCIENCE TO POLICY: HOW MUCH KNOWLEDGE IS NEEDED?

An Ecosystem Approach to Fisheries (EAF) requires policy makers to take account of a wide range of fisheries impacts when setting objectives, and these should be supported by reliable scientific advice (Garcia and Cochrane, 2005; Jennings, 2005). Given the complexity of ecosystems in which target species are embedded, an EAF requires extensive ecosystem knowledge (e.g. Pikitch et al., 2004). Therefore, while under traditional single-species fisheries management science is mostly 'ahead of policy', science is likely to 'lag behind' when adopting an EAF (Rice, 2011; Depestele, 2015). Further, scientific insights often trigger new research questions, requiring more research. Or, as Albert Einstein knew, '*The more you learn, the more you realize how much you don't know*'. This certainly also applies to research on ecosystem structure and functioning, as seen in the thesis at hand.

But how much knowledge is enough in order to apply an EAF? The notion that ecosystems are complex, and that the impact of fisheries is hard to predict, creates uncertainty on how to implement an EAF in the real world (Sagarin and Crowder, 2009). As a consequence, according to Pauly (in Hume, 2006), research is often publicly funded as an alternative to political action, in the assumption that more ecosystem knowledge is needed before an EAF can be implemented. However, the current crisis in fisheries is not caused by lack of scientific information, but because a holistic view of ecosystems is missing (Bundy et al., 2008). Therefore, science alone is not the answer. We need a governance model for fisheries that stimulates action based on the available knowledge, rather than one that focuses on missing information (Frid et al., 2006; Sagarin and Crowder, 2009).

In an ecological economics worldview (see Box 1 in Chapter 1), we should not only recognize that fisheries resources are limited (e.g. Rees, 2003), but also that science will never fully account for the complex ecological reality in which fisheries operate (Bundy et al., 2008). This ever existing knowledge gap should, however, not be an obstacle to start the EAF process. According to the FAO (2016), a successful application of an EAF uses science as a basis for policy, and accounts for uncertainty where knowledge still falls short. This can be achieved in two ways. First, an EAF has to embrace a precautionary approach to management, adopting risk-based frameworks (e.g. Pikitch et al., 2004). Second, it also has to be an adaptive process, incorporating new information in management as it becomes available (FAO, 2016a). In this way, consensus on the application of an EAF will come through 'experience gained in actions implemented' (Fluharty, 2005). As such, EAF has to be a dynamic process of constant evaluation and improvement, rather than a faraway and seemingly impossible goal to achieve.

2 AN ECOSYSTEM APPROACH TO SEABOB FISHERIES IN SURINAME

An EAF takes a holistic view on ecosystems, and the way fisheries interact with them (e.g. Garcia and Cochrane, 2005). Considering the various indirect ecological and socio-economic impacts of fishing, an EAF should essentially consider the following three aspects, as outlined in Chapter 1 (Pauly and Chuenpagdee, 2002):

1) The **trophic relationships** between exploited species and the food sources on which they rely;

2) The **competition between fishing fleets**, that might express itself through bycatch or trophic linkages between species targeted by different fleets operating in the same ecosystem;

3) The direct and indirect **impacts of fishing on habitats and species communities**.

2.1 THE MAIN SCIENTIFIC FINDINGS OF THE THESIS

This doctoral thesis included research on the **ecosystem**, and on **fisheries impact** on the ecosystem (Fig. 1). Ecosystem research included a characterization of the benthic assemblages and habitats of the inner Suriname Shelf (**ecosystem structure – objective 1**), and an assessment of the role of *Xiphopenaeus kroyeri* in the coastal food web (**ecosystem functioning – objective 2**). Further, the impact of *X. kroyeri* trawling on ecosystem structure and functioning was studied (**ecosystem impact – objective 3**) (Fig. 1). *Targeting these objectives, the findings of this thesis answer key questions related to the three main aspects of an EAF.*

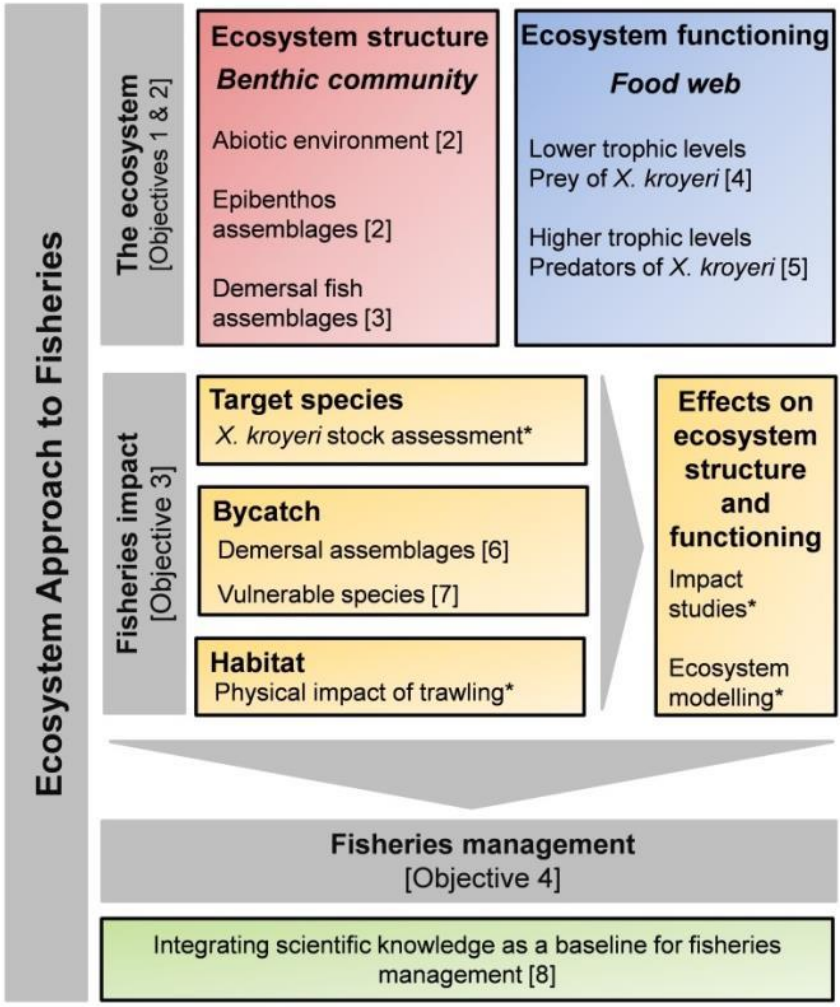

Figure 1. Theoretical framework of the doctoral thesis. Structural (Objective 1) and functional (Objective 2) ecosystem features were studied, and the way they are impacted by fisheries (Objective 3). The resulting information is discussed in a management context (Objective 4). Numbers between brackets denote the respective chapters in which the different topics were addressed. Aspects not included in this thesis are marked with an asterisk (*).

2.1.1 TROPHIC RELATIONSHIPS

Regarding trophic relationships, the main question that should be considered in an EAF in the seabob fishery is:

Q: What are the prey and predators of* X. kroyeri*?

It appeared that *X. kroyeri* feeds opportunistically on a range of animal prey taxa, mainly hyperbenthic crustaceans. Further, benthic microalgae growing on intertidal mudflats are a main contributor to the diet of adult, juvenile and postlarval stages of the shrimp (Chapter 4). On the other hand, we found that *X. kroyeri* is an important prey species for several abundant demersal fish species (Chapter 5). Given the fact that this shrimp is the only abundant epibenthic mid-trophic level species, and that it feeds on a variety of food sources and is eaten by many demersal fish species, we concluded that *X. kroyeri* has a key function in channeling energy from lower to higher trophic levels, in a 'wasp-waist' pattern (Chapter 5).

2.1.2 COMPETITION BETWEEN FISHING FLEETS

Competition between fishing fleets operating in the same ecosystem might express itself through bycatch, or through trophic linkages between species targeted by different fleets. As such, important questions for an EAF in the seabob fishery are:

Q: Does the seabob fishery affect target species of other fisheries through bycatch?

Q: Do target species of other fisheries rely on* X. kroyeri *as food?

We found that *X. kroyeri* indeed constitutes an important food source for several demersal fishes (mainly Sciaenidae), which are targeted by the coastal artisanal fishing fleet (Chapter 5). Further, juvenile commercial fishes are plentiful in the (discarded) bycatch of seabob fisheries (Chapter 6). As such, both through target catch and bycatch, seabob fisheries might interact with the artisanal fishing fleet. The significance of these interactions, however, remains to be assessed.

2.1.3 IMPACT ON HABITATS AND SPECIES COMMUNITIES

To date, ecological research on the benthic ecosystem of the Suriname continental shelf is very limited. So before being able to assess the impact on the ecosystem, it is important to know what is there. A first question that should thus be answered in order to apply an EAF is:

Q: What benthic habitats and species communities occur on the inner Suriname Shelf?

This knowledge gap was tackled by an extensive trawl survey, in which benthic communities were sampled year-round, together with several environmental parameters. The main outcome of this trawl survey was a clear inshore to offshore zonation in abiotic characteristics, and assemblages of both epibenthos (Chapter 2) and demersal fish (Chapter 3). Longitudinal east – west variation and temporal differences were of much less importance. While water parameters changed rather gradually towards the offshore zone, bottom characteristics shifted abruptly between the 20 and 30 m isobath. This sudden change was reflected in the distribution of demersal assemblages. The inshore waters below 30 m are characterized by a muddy seabed, harboring a species-poor epibenthic community, largely dominated by the seabob shrimp *X. kroyeri*. Conversely, the same area is home to a diverse assemblage of demersal fishes, known as a 'tropical sciaenid community'. Beyond the 30 m isobath, on sandy substrates, demersal assemblages are very different, with high epibenthic species diversity, no *X. kroyeri*, and demersal fishes typical of deeper shelf communities. The shift from *coastal* to *offshore* assemblages of epibenthos and demersal fish was the most important feature of the benthic community, coinciding with a transition between a coastal, river influenced system and an open shelf system. In the coastal ecosystem, *X. kroyeri* plays a dominant structuring role in the benthic community. Further, these shallow waters are home to many juvenile fishes, suggesting a main nursery function for demersal fish populations.

Once we know what is there, the impact of the fishery on the ecosystem can be assessed, which raises the following question:

Q: How does the seabob fishery affect benthic habitats and species communities on the inner Suriname Shelf?

The abiotic characterization of the inner Suriname Shelf (Chapter 2) revealed that the seabed in the area where seabob trawling takes place is characterized by unstable sediments, with high mud contents, and no habitat-structuring macro- or epibenthic species. Therefore, we focused on the impact of fisheries on species communities, rather than habitats, by analyzing the catch composition of commercial seabob shrimp fisheries (Chapter 6). Despite being relatively selective for a tropical shrimp fishery, we found that the Suriname seabob fishery still produces considerable amounts of bycatch (on average 41% of the catch by weight). In congruence with our finding that the epibenthic community is species-poor and dominated by *X. kroyeri* (Chapter 2), bycatch of epibenthos only represented 2% of the catch. The bulk of the bycatch was fish, accounting for 31% of the total catch. Fish bycatch mainly consisted of

small ‘trash fish’, which is discarded. Further, several vulnerable elasmobranch species are regularly caught. While we found that the current gear adaptations, Turtle Excluded Devices (TEDs) and Bycatch Reduction Devices (BRDs), cause a significant reduction in the capture of large-sized rays, many small-sized rays remain being caught (Chapter 7). Although the amounts of discarded fish are substantial, the impact of this discarded bycatch on the population of the bycaught species remains to be assessed.

2.2 IMPLICATIONS FOR MANAGEMENT OF THE SEABOB FISHERY

As fourth objective, this doctoral study aimed to translate the obtained scientific knowledge into recommendations for fisheries management (Fig. 1). The management of the Suriname seabob fishery currently has measures in place related to (1) spatio-temporal operation of the fishery, (2) fishing effort, (3) gear-related aspects of the fishery and (4) governance (LVV, 2010). In the following paragraphs, each of these aspects is evaluated in the light of the results obtained in this doctoral thesis.

2.2.1 SPATIO-TEMPORAL MANAGEMENT MEASURES

SPATIAL FISHING RESTRICTIONS: *Legal seabob trawling zone: within Suriname's EEZ the operation of seabob trawlers is spatially restricted to the area delimited by lines nominal to the 10 and 15 fathom water depth (resp. 18 and 27 m), extending to 18 fathom (33 m) in the eastern part of the EEZ (see Fig. 8 in Chapter 1).*

RECOMMENDATION: The seabob trawling zone should be maintained, and especially the lower depth limit at 10 fathoms is important to preserve.

RATIONALE: We found that the area where seabob trawl fisheries take place is characterized by muddy substrates which harbor species-poor *coastal* and *transition* epibenthic assemblages, without habitat-structuring species (Chapter 2). In this environment, the physical impact of bottom trawling on the seafloor is expected to be low. Although trawls in the seabob fishery are equipped with tickler chains on the ground rope, the gear is still comparatively light (Southall et al., 2011). Further, the 'estuarine like' conditions in the area up to 30 m depth are likely to cause a high degree of natural environmental perturbation (Elliott and Quintino, 2007), including deposition and resuspension of fine sediments by tides and currents, causing turbid waters and an unstable seabed (Eisma et al., 1991; Nittrouer and Demaster, 1996). As such, seabob fisheries operate in a naturally dynamic environment. While *X. kroyeri* thrives in this system, few other epibenthic species are present, the macrobenthos seems poorly represented, and bottom trawling is not likely to have a major physical impact. The location of the current seabob trawling zone therefore seems adequate to minimize effects of the fishery activities on the habitat.

Species-rich *offshore* epibenthic assemblages occur beyond the 30 m isobath. Here, the seabed is sandy and the benthic communities and habitats are likely more vulnerable to trawling (Chapter 2). Although trawl fisheries for finfish and

Penaeus sp. shrimp operate in this area (Bhagwandin, 2012), the upper depth limit to the seabob trawling zone avoids seabob trawlers entering this more offshore area. Still, while we recommend maintaining this upper limit to the seabob trawling zone, there is probably little risk for violation of this depth limit by seabob trawlers, as *X. kroyeri* is practically absent beyond the 30 m isobath. In contrast, *X. kroyeri* occurs abundantly below the lower 10 fathom depth limit (Chapter 2), which poses a risk of non-compliance with this inshore limit to the seabob trawling zone. Our results have shown that the shallow near-shore waters are home to many juvenile fish (Chapter 3), and act as 'nursery grounds' (Blaber et al., 1995; Blaber, 2002). The ban on seabob trawling (and all other bottom trawl fisheries) below the 18 m (10 fathom) isobath is therefore a very valuable management measure to protect coastal fish stocks and to avoid direct interaction with the artisanal fishing fleet.

IMPLEMENTATION: Compliance with spatial restrictions should be controlled at the Fisheries Department through the Vessel Monitoring System (VMS).

CONSIDERATIONS: Based on the abiotic characteristics of the seabed (Chapter 2), we judged that seabob trawling is unlikely to cause important physical damage to benthic habitats. Nevertheless, assessments of fisheries impact typically require control-impact studies, in which areas with different degree of fisheries impact (e.g. number of passages of trawling gear over the seabed) are directly compared (e.g. Collie et al., 2000). When overlaying the 15 locations sampled during the trawl survey (see maps in Chapters 2 and 3) with the 'heat map' of seabob trawling effort (Fig. 9 in Chapter 1), locations of different cumulative fishing intensity were sampled during the survey. The eastern 'Ma-transect' was located in an intensively trawled area, while fishing effort was much lower in the areas of the other two transects ('Su' and 'Co'). The fact that the eastern 'Ma-transect' differed little from the other two transects in characteristics of the seabed and in demersal assemblages of epibenthos and fish (Chapter 2 and 3), might indicate that seabob trawling has little measurable effects on benthic habitats and species communities. This conclusion, however, might be flawed for two main reasons. First, within the delimited depth zone (18 to 27-33 m), seabob trawl fisheries are allowed to operate over the entire width of the Suriname EEZ. Still, effort is concentrated in certain 'hotspots' (Fig. 9 in Chapter 1). Because seabob trawlers always aim to maximize catches (Pérez, 2014), it appears that the areas of high trawling intensity have higher shrimp densities. This might indicate underlying abiotic differences in these areas, which favor higher shrimp densities. Consequently, the areas of lower fishing intensity (the 'Su' and 'Co' locations) are unsuitable reference sites to draw conclusions on the environmental impact of fisheries. Second, whereas the 'Su' and 'Co' locations represent areas of lower trawling intensity, they might nevertheless be trawled every once in a while. This can be enough to prevent the recovery of benthic species or habitats (e.g. Williams et al., 2010), adding to the fact that these are unsuitable 'control' sites to adequately assess trawling impact. This second aspect relates to a fundamental

difficulty involved in studying fisheries impact. While present day impacts of fisheries can effectively be measured, the historical effect of fisheries is often hard to assess due to a lack of 'pristine' baseline reference areas (Thurstan et al., 2010). Further, trawl fisheries themselves might create systems dominated by resilient, fast growing species and little remaining physical habitat structure (e.g. Tillin et al., 2006). As a consequence, the ecological impact of fisheries activity on these systems nowadays might be low. Nevertheless, fisheries have severely altered many benthic ecosystems from their original state (Pinnegar and Engelhard, 2008).

FURTHER RESEARCH: In the neighboring country French Guiana, no industrial trawl fisheries for seabob shrimp take place, and all bottom trawling is prohibited below the 30 m depth contour (Banks and Macfadyen, 2010). As such, suitable untrawled reference sites are likely to be present, allowing for a better assessment of the impact of seabob trawling on benthic habitats and species communities.

TEMPORAL FISHING RESTRICTIONS*: No closed fishing season, seabob trawling is allowed year-round.*

RECOMMENDATION: Analyze temporal stock dynamics

RATIONALE: Our results have shown that, despite large fluctuations in environmental parameters such as river outflow, little temporal variation occurs within the assemblages of epibenthos and demersal fish (Chapter 2 and 3). This is also reflected in the seabob fishery, which has rather constant catches throughout the year (Pérez, 2014). In contrast, in the neighboring country Guyana, the seabob fishery closes off each year for six weeks in the period August – September, due to the CPUE generally being low in this period. It is an industry-based management measure, and the start of the closure is decided upon agreement between different stakeholders in the fishery (J. Jagroop, pers. comm.). While the seabob is 'allowed to recover' in this period, the closure of the seabob fishery in Guyana is based on economic rather than ecological grounds. Nevertheless, ecological insights on the temporal dynamics of the seabob stock off Suriname (and Guyana) might have important consequences for fisheries management as well. Notably, studies on the life cycle and growth of *X. kroyeri* in the region are necessary to identify periods when fishing should be reduced (e.g. when a large proportion of the females is gravid), in order to allow for maximal recruitment and increased fisheries yields in the rest of the year.

IMPLEMENTATION: A large amount of data is currently available on the size-composition, sex-ratios and maturity of commercial seabob catches

(Landburg, 2013; Pérez, 2014). A thorough analysis of these data should allow to identify temporal patterns in the population of *X. kroyeri* off Suriname.

FURTHER RESEARCH*:* Additional insights on temporal stock dynamics may result from detailed studies on the life cycle of *X. kroyeri* in the region.

SPATIO-TEMPORAL BYCATCH MANAGEMENT*:* *No spatial or temporal fishing restrictions related to bycatch*

RECOMMENDATION*:* **Imply a 'move-on rule' to reduce bycatch ratios**

RATIONALE: Despite the use of gear adaptations (TED and BRD) bycatch in the seabob fishery might still be considerable. Bycatch on average represents 41% of the catch by weight, but bycatch ratios are typically variable in space and time (Chapter 6). To avoid situations with excessive bycatch ratios, a management measure could be applied which requires trawlers to change location ('move-on') when bycatch ratios pass a certain threshold value, or when vulnerable species (e.g. rays) are numerous in the bycatch.

IMPLEMENTATION: Acceptable threshold values of overall bycatch and bycatch of vulnerable species will have to be decided upon by stakeholder agreement. Compliance with the move-on rule could be controlled by sea-going observers from the Fisheries Department, and by coastguard patrols.

CONSIDERATIONS: Compliance with a move-on rule might be difficult to secure. A successful application will depend on a trust-relationship with captains in the seabob fishery, which might be accomplished by involving them closer in management decisions. Given the variability of bycatch ratios in the seabob fishery (Chapter 6), a move-on rule is appropriate to instantly react to excessive amounts of bycatch. On the other hand, areas or periods with consistently high bycatch ratios might be identified through continued data collection. This can lead to spatial or temporal fishing restrictions, to be controlled through VMS.

FURTHER RESEARCH*:* More data on discarded bycatch should be collected by sea-going observer programs, in order to better assess spatio-temporal variability in bycatch ratios, and identify potential areas which should (temporarily) be avoided by the fishery.

2.2.2 FISHING EFFORT MANAGEMENT MEASURES

INPUT CONTROL: *A Harvest Control Rule (HCR) specifies the maximum fishing effort (in days-at-sea; DAS) in relation to the catch-per-unit-effort (CPUE, in tons per day). A maximum of 5,100 DAS is allowed, when CPUE is at or above the trigger point of 1.48 t/day. When CPUE falls below this point, DAS should decrease linearly according to the formula specified in the HCR (see Fig. 7 in Chapter 1).*

RECOMMENDATION*:* Do not exceed the effort specified under the current HCR and update HCR with available data

RATIONALE: The allowable fishing effort defined under the current HCR seems adequate, as CPUE has been relatively constant over the years (see Fig. 11 in Chapter 1; Pérez, 2014). We found that *X. kroyeri* plays a key role in the functioning of the coastal food web, channeling energy from low trophic levels up the food chain (Chapter 4 and 5). As such, although the seabob stock seems to cope with the current rate of exploitation, fisheries might have wider ecosystem consequences, altering the trophic network and the flow of biomass and energy through the system (e.g. Branch et al., 2010). Notably, overexploitation of *X. kroyeri* could have substantial effects on the productivity of higher trophic level demersal fishes. Seabob fisheries can therefore negatively affect the artisanal fishing fleet targeting these demersal fishes. To avoid these ecological and socio-economic consequences of seabob trawling, the status of the stock should be closely monitored. This is done in the Seabob Working Group (SWG), which gathers monthly and evaluates the actual CPUE in relation to the HCR. A HCR has the great advantage that the concept is easy to understand for all stakeholders involved in the management of the fishery (e.g. Froese et al., 2011). We therefore recommend continuing the use of a HCR to evaluate the stock status, and adjust effort accordingly. However, given the importance of *X. kroyeri* as a potential wasp-waist species, we advise a precautionary approach to the effort specified by the HCR, and an update of the HCR with the best available information in order for the stock assessment to accurately reflect real stock biomass.

IMPLEMENTATION: Whereas a large amount of data on the size-composition, sex-ratios and maturity of commercial seabob catches is available (Landburg, 2013; Pérez, 2014), it is not used in the current stock assessment model because the data is not well organized and cross-checked (CRFM, 2009; P. Medley, pers. comm.). A sound data management system should relief this problem, and allow for updates of the stock assessment to take into account as much relevant data as possible. Further, it seems appropriate for the HCR to consider a different measure of fishing effort. Days-at-sea includes time spent steaming and break-down trips, and therefore does not accurately reflect effort, which might be better represented by hours of effective trawling.

CONSIDERATIONS: Our research on predators of *X. kroyeri* (Chapter 5) has revealed its importance as a food source for commercially important demersal fishes. On the other hand, although no stock assessments for these fishes are available, their populations are likely suppressed due to heavy exploitation by the coastal artisanal fishing fleet (Charlier, 2000). This might relieve top-down control on shrimp populations, and allow for a sustainable exploitation of *X. kroyeri* without affecting food availability for fish. The importance of the indirect trophic interaction - through *X. kroyeri* - between seabob fisheries and artisanal fisheries remains unknown. Similarly, the minimum size of the stock of *X. kroyeri* to be maintained in order to ensure its key wasp-waist function, is unclear. Consequently, while it is essential for fisheries management to recognize the importance of *X. kroyeri* for ecosystem functioning, based on our results, we cannot define 'safe levels' of exploitation which should be respected to avoid negative ecological or socio-economic consequences of seabob fisheries.

The functional importance of *X. kroyeri* in the ecosystem, as revealed in this thesis, also triggers the question as to what drives the abundance of this species in the ecosystem. Little is known on the life cycle and reproduction of *X. kroyeri* in Suriname (Torrez, 2015). Recruitment in penaeid shrimp is often heavily influenced by environmental factors, causing bottom-up population regulation (e.g. Galindo-Bect et al., 2000; Moller et al., 2009). The influence of environmental variation on populations of *X. kroyeri* off Suriname, including seasonal variation in the freshwater outflow of domestic rivers or the outflow of the Amazon River, is yet to be assessed. Likewise, whereas events of massive influx of *Sargassum* seaweed to the Guianan Ecoregion in recent years (e.g. Smetacek and Zingone, 2013) have been associated with periods of decreased CPUE in the seabob fishery (LVV, 2015), a causal link has not been demonstrated. It could be argued that little is to be gained for fisheries management in understanding the influence of environmental factors on shrimp populations because the driving factors cannot be altered. Importantly, and according to the HCR, fishing effort should be reduced when shrimp - for whatever reason - become scarcer (LVV, 2010). Nevertheless, defining whether reduced CPUE is caused by fishing activity or environmental factors, i.e. by factors that can be controlled or not, is important to make correct ecosystem-based management decisions. Further, understanding the effect of environmental variables on *X. kroyeri* might allow making predictions on shrimp catches, with economic benefits for the fishery.

Based on the morphological data analyzed so far, 'Suriname seabob' is treated as a single stock in the stock assessment and HCR, different from the seabob stock in Guyana (CRFM, 2009; Southall et al., 2011). However, no data on seabob populations off French Guiana have been taken into account. It seems likely to assume that the 'Suriname seabob' stock is, at least partly, shared with the neighboring countries, like other fish and shrimp resources on the Guyanas-Brazil Shelf (CRFM, 2009). Further, the species *Xiphopenaeus kroyeri* has been

found to contain different cryptic (sub)species (Gusmao et al., 2006; Gusmao et al., 2013). Population status and genetics of *X. kroyeri* off Suriname clearly require further investigations, which might reveal relevant information for stock assessment and fisheries management.

FURTHER RESEARCH*:* Mass-balance ecosystem models (e.g. Ecosim with Ecopath; Christensen and Pauly, 2004) should allow for a more quantitative assessment of the key trophic function of *X. kroyeri* in the ecosystem, and the interactions between fishing fleets through trophic links with *X. kroyeri.* Further, studies on the species' life cycle, and the influence of environmental factors are expected to bring relevant information for a sustainable management of the seabob fishery. Finally, further research on morphological and genetic characteristics should clarify the status of 'Suriname seabob' as a single stock as it is treated now in stock assessments (CRFM, 2009).

OUTPUT CONTROL*: No output control measures (e.g. total allowable catch) apply to the Suriname seabob fishery*

RECOMMENDATION: Further research needed to confirm the validity of the lack of output control to the seabob fishery

RATIONALE: In the HCR, CPUE is used as a proxy for stock biomass, which is a reasonable and widely used assumption (e.g. Quirijns et al., 2008). Nevertheless, it might be safer to have additional ways of estimating stock biomass and controlling fishing effort, in order to avoid overfishing. In the HCR, allowable fishing effort is calculated based on CPUE. This means that fishing effort can remain high as long as CPUE is high, whatever the total stock biomass. Theoretically, this could allow for stock depletion if an increasingly smaller stock is concentrating on the trawling grounds, where a high CPUE is maintained despite an overall smaller stock size. The non-linear relationship between CPUE and total stock biomass might also be obvious from Fig. 11 in Chapter 1. While variable fishing effort would presumably lead to fluctuations in stock biomass, the CPUE in the seabob fishery has remained fairly constant over the years. Clearly, factors other than total stock biomass (e.g. the actual density of shrimp on the fishing grounds) might influence the CPUE.

IMPLEMENTATION: As a first step, landings data could be coupled to VMS data, to gain insight in the spatial distribution of catches (e.g. Hintzen et al., 2012)

FURTHER RESEARCH: Mass-balance ecosystem modelling (e.g. Ecosim with Ecopath; Christensen and Pauly, 2004) should yield estimates of the minimum seabob stock biomass in order for the species to maintain its pivotal function

in the coastal food web. This 'minimum required biomass' could then be used to assess whether the current rate of exploitation (8,000 to 10,000 tons/year) is likely to severely affect ecosystem functioning, or whether catch quota should be implemented.

2.2.3 GEAR-RELATED MANAGEMENT MEASURES

TED AND BRD: *Bycatch in the Suriname seabob fishery is currently tackled through the obligate use of Turtle Excluder Devices (TEDs) and square-mesh panel Bycatch Reduction Devices (BRDs).*

RECOMMENDATION: Optimize fishing gear to further reduce bycatch

RATIONALE: TEDs and BRDs have proven very effective in bycatch reduction. On average, BRDs cause a 34%-reduction in the bycatch of small teleost fishes (Polet et al., 2010), while we have found that the TEDs cause an average 36%-reduction in the overall bycatch of five ray species (Chapter 7). In general, the Suriname seabob fishery now produces low bycatch levels for a tropical shrimp fishery (e.g. Andrew and Pepperell, 1992; EJF, 2003; Gillett, 2008). Nevertheless, bycatch on average still represents 41% of the catch by weight. About three quarters of this bycatch are fish, most of which is discarded. This fish includes species of commercial interest to the artisanal fishing fleet, and elasmobranch species of conservation concern (Chapter 6).

IMPLEMENTATION: Bycatch reduction could be accomplished by additional technical gear adaptations. In this respect, we would recommend trials with Nordmøre-grids. Unlike TEDs, these grids have a small bar-spacing (in the order of 2 cm) that allow the targeted shrimp to pass through, while bycatch is forced out of the trawl by an escape opening on the upper side of the codend. Nordmøre-grids are widely used in trawl fisheries for Northern shrimp *Pandalus borealis* (e.g. He and Balzano, 2012), a species that is similar in size to *Xiphopenaeus kroyeri* (Holthuis, 1980). Moreover, they have proven to effectively reduce bycatch, while maintaining shrimp catches, in seabob trawl fisheries in Brazil (Silva et al., 2012a). Other bycatch reduction devices that have been successfully applied in shrimp trawls similar to the ones used in the seabob fishery include composite-panel and nested-cylinder BRDs (Parsons et al., 2012; Parsons and Foster, 2015). However, these BRDs are mainly aimed at excluding small teleost fish, and are unlikely to mitigate bycatch of (small-sized) rays as well (D. Foster, pers. comm.). In contrast, due to their small bar-spacing, Nordmøre-grids are likely to exclude rays, teleost fish, and jellyfish.

CONSIDERATIONS: Next to modifications to the current trawls, a re-evaluation of the entire gear might be needed. In European bottom trawl fisheries for Brown shrimp *Crangon crangon,* bycatch is now effectively being reduced by

the use of electrodes on the ground rope which create electric pulses (Polet et al., 2005). In this way, the shrimp are stimulated to 'jump up' from the seabed, allowing the trawl to fish somewhat higher in the water column, which reduces bottom impact and bycatch of benthos and flatfish (Soetaert et al., 2015). With respect to the Suriname seabob fishery, application of this technique might be effective in reducing bycatch of ground-dwelling rays. Nevertheless, teleost fishes make up the bulk of the bycatch in the seabob fishery, and typically reside somewhat higher in the water column. The otter trawls currently used in the seabob fishery have a vertical opening of approximately 2 m (B. Verschueren, pers. comm.), while the shrimp are at or just near the bottom (Freire et al., 2011). Therefore, overall bycatch reduction is likely to be more effective by fishing closer to the seabed, and by reducing the vertical trawl opening. Gear with a lower vertical opening will also lessen drag through the water, reducing fuel consumption (Suuronen et al., 2012). Moreover, the application of pulse-fishing techniques might be to complex and expensive for application in the current seabob fleet, which is consists of very old vessels.

While the numbers of discarded fish in the Suriname seabob fishery are substantial, the current level of information does not allow quantifying the impact of bycatch mortality on the populations of these bycatch species, and on the fisheries that target them. For none of the bycatch species, stock assessment or population estimates are available. Therefore, in the absence of 'safe' limits to bycatch, minimizing bycatch as much as possible is recommended as a precautionary management measure. Nevertheless, as bycatch in trawl fisheries can never be completely avoided, the fishery could also look for ways to make use of the bycatch, in order to reduce the wastage of food (Gillett, 2008).

Fish bycatch in the seabob fishery often constitutes an important extra source of income for captains and crew, who receive additional payment for landed commercial fish (S. Hall, pers. comm.). In the informal circuit, high prices are also paid for dried fish swim bladder (up to 300 USD per kg; K. Bilo WWF Guianas, pers. comm.). Clearly, bycatch reduction will have financial consequences for the fishermen. This should be acknowledged, and appropriate compensations measures should be taken along with efforts to reduce bycatch.

FURTHER RESEARCH: Like target catch, quantifying the effect of bycatch on overall ecosystem functioning, and on the productivity of other fisheries, will require mass-balance ecosystem models (e.g. EwE; Pauly et al., 2000). Further, stock assessments of the common commercial bycatch species will allow estimating the impact of bycatch mortality in the seabob fishery on these stocks.

2.2.4 GOVERNANCE

STAKEHOLDERS MEETING: *The Seabob Working Group (SWG) overlooks the implementation of management measures in the Suriname seabob fishery. The SWG gathers monthly, bringing together representatives from the fishing industry, the artisanal seabob fleet, the LVV Fisheries Department and NGO's (the World Wildlife Fund; WWF)*

RECOMMENDATION: Continue the SWG

RATIONALE: Like all management frameworks, EAF is a people-based process, and stands or falls with the actions taken by stakeholders (FAO, 2016a). As such, seeking consensus on the actions to be taken in the fishery is a vital part of fisheries management. Only with an agreement among all parties involved in the fishery, management measures are likely to be effectively applied.

CONSIDERATIONS: Organizing regular meetings among stakeholders does not automatically lead to effective management. Yet, the Seabob Working Group seems to efficiently tackle issues in the fishery. An important driving factor for the activities discussed in the SWG is the 'Research and Development (R&D) plan' for the seabob fishery. This plan is based upon the yearly milestones that the fishery should reach regarding the six conditions that were set upon MSC certification. Each SWG meeting, the progress agains the R&D plan is discussed, and activities are agreed upon. Further, each meeting, the latest CPUE data are presented and evaluated against the HCR. As such, the SWG is closely monitoring the stock status, and can act quickly in case the CPUE goes down. Besides the R&D plan and the HCR, miscellaneous issues in the fishery are discussed (e.g. issues with rising fuel prices, problems with *Sargassum* seaweed invasions,...). Further, the SWG organises some informal activities (e.g. a yearly christmas dinner), which creates a familiar atmosphere. This enhancing communication among the different stakeholders (also outside the SWG meetings), which, in turn, enhances the understanding of eachothers actions and decisions. This 'human behaviour' aspect and mutual understanding between representatives from the fishery and the government and NGOs is crucial for effective fisheries management (Fulton et al., 2011).

3 CONSIDERATIONS FOR AN EAF IN SURINAME

3.1 MSC ECO-LABELLING AND THE EAF: LESSONS LEARNT

This doctoral study was directly motivated by conditions raised during the assessment of the Suriname seabob fishery against the principles and criteria of the Marine Stewardship Council (MSC) in 2011. Three of the six certification conditions to the fishery (see Box 5 in Chapter 1) related to a lack of understanding of the ecosystem impacts of seabob trawling on the Suriname Shelf (Southall et al., 2011). The information provided in this thesis allowed for an improved assessment of these impacts.

After the initial assessment and certification of the fishery in 2011, the certifier conducted yearly surveillance audits to assess the progress on the six certification conditions. These audits were either conducted onsite (in Suriname), or through conference calls. Before each audit, the latest available information on all certification conditions (including the three conditions addressed in this thesis) was provided to the assessment team. The canditite was consulted extensively during each of these audits, together with all other stakeholders in the fishery, including the LVV fisheries ministry, respresentatives from the artisanal fishery and NGOs. Upon the 4th surveillance audit, the draft version of this thesis was provided to the assessment team. The report of this audit concludes that all six conditions of the fishery can be closed (Southall et al., 2016). Currently, the assessment for re-certification of the fishery is ongoing. If the fishery is re-certified, new certification conditions may apply.

Based on the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) and input of environmental organizations and fisheries experts worldwide, the MSC principles and criteria represent a widely recognized standard for ecological sustainability (Gulbrandsen, 2009). Further, by applying conditions to certification, the MSC certification procedure recognizes EAF as an adaptive process of constant improvement. Nonetheless, like other eco-labelling initiatives, e.g. FSC in forestry (Clark and Kozar, 2011), MSC has received criticisms related to the credibility of the program (e.g. Jacquet et al., 2010b). This critique mostly relates to scoring against the MSC principles as being too generous, which would result in fisheries being incorrectly certified as 'sustainable' (Stokstad, 2011). Environmental NGOs have therefore filed formal objections against several MSC certifications (Christian et al., 2013).

In 2011, WWF International raised an objection against the pending MSC certification of the Suriname seabob fishery. This led to a adjudication process, in which the adjudicator confirmed the determination by the certifier that the fishery was eligible for certification (Southall et al., 2011). Nevertheless, a hypothetical loss of this trial might have resulted in the Suriname seabob fishery leaving the MSC program (C. Meskens, pers. comm.), and abandoning several management measures that were put in place to meet the MSC standard. Based on this experience with the MSC program as an instrument to implement an EAF, certification early in the EAF process is likely to yield more net benefits than an overly rigorous scoring against the sustainability criteria. MSC certification creates increased market access, and provides fisheries with appropriate recognition for the efforts taken in implementing sustainable management practices (Gulbrandsen, 2009). Early certification should, however, go together with a reinforced system of certificate conditions, and progress against the improvement trajectory should be well monitored (Sampson et al., 2015). In general, it could be argued that fishery eco-labelling should value the 'progress on the path to sustainable management' as much as the actual performance against sustainability standards. This approach might be especially effective in developing world countries where many fisheries are poorly managed, cannot meet current eco-labelling standards, and are in need of an improved market access (Sampson et al., 2015).

The Suriname seabob is the only MSC-certified fishery in the region, and one of the few tropical fisheries with this ecolabel (MSC, 2016). Under impulse of the MSC certification scheme, a management plan for the Suriname seabob fishery has been established, which is adopted in national fisheries legislation. The current management of the Suriname seabob fishery involves sound management measures supported by scientific advice and a stakeholders meeting to ensure a proper application of management measures. Further, the fishery actively supports research, in order to fill knowledge gaps related to the ecosystem supporting the fishery. The management of the seabob fishery can therefore serve as an example for other fisheries in the country, and even in the wider region.

MSC certification involves a high cost for the fishery, mainly related to the yearly assessments that have to be undertaken. These costs might be excessive for many small scale and developing world fisheries, hampering an entry into the MSC program (e.g. Sampson et al., 2015). On the other hand, management measures that favour sustainable resource management have benefits going beyond the market incentive for eco-labelled products. Essentially, the measures taken to comply with the MSC standard should allow for a long-term sustainable exploitation of the fishing resource.

3.2 A WIDER APPLICATION OF EAF IN SURINAME

In order to successfully apply an EAF, a holistic view on ecosystems and the fisheries that interact with them is fundamental (e.g. Garcia and Cochrane, 2005). Whereas this doctoral thesis focussed on the seabob fleet, this fishery is clearly not isolated from other fisheries in Suriname. Notably, within the river-influenced coastal ecosystem (up to ca. 30 m depth) (Chapter 3), the seabob fishery might indirectly interact with the coastal artisanal fishing fleet, through trophic interactions (Chapter 5) and through bycatch (Chapter 6). Essentially, both fisheries should be considered together in order for management measures to be effective. A better management of Suriname's artisanal fisheries is therefore a major future challenge for fisheries management. Artisanal fisheries generate a lot of employment and account for ca. 70% of the country's fisheries landings (Bhagwandin, 2012), but they suffer from overcapacity and declining catches (Charlier, 2000; M. Lall, pers. comm.).

An EAF should also consider the various interactions that might exist between fisheries and the ecosystem. Although we evaluated that seabob trawling has little impact on benthic habitats and epibenthic communities, this might not be the case for trawl fisheries operating further offshore, where diverse *offshore* epibenthos assemblages occur (Chapter 2). In this area, a large trawling fleet used to target *Penaeus sp.* shrimp, but this fishery has now collapsed, and is not recovering till today (see Fig. 6 in Chapter 1) (Bansie R., 2010; LVV, 2013). Recruitment overfishing might be a major cause of the decline of *Penaeus sp.* stocks off Suriname (e.g. Gracia, 1996). On the other hand, fishing activity might have severely altered the offshore benthic ecosystem off Suriname, hampering recovery of the *Penaeus sp.* fishery. In contrast to the seabob fishery, impact on benthic habitats and communities might be considerable in bottom trawl fisheries operating beyond the 30 m isobath on the Suriname Shelf. This impact should be taken into account for the application of an EAF in Suriname.

By studying the food sources of *X. kroyeri*, we found that primary production on intertidal flats is a main energy and carbon source for the species (Chapter 4), and therefore indirectly also for many demersal fish species which feed on *X. kroyeri* (Chapter 5). While Bianchi (1992a) stated that the coastal, river influenced ecosystem off the Guianas is fueled by detritus, this thesis revealed that primary production on the extensive intertidal mudflats in the area might provide a major primary source as well. Protection of the natural coastline, where mangroves trap sediments and create intertidal mudflats (Augustinus, 1978; Alongi, 2008) thus seems an important consideration for fisheries management in Suriname. Degradation of these coastal habitats might cause a reduced food supply for *X. kroyeri*, leading to a decreased productivity in coastal fisheries as a whole.

In practice, for a wider application of an EAF in Suriname, improvements are required in all the different fishing fleets, including artisanal and industrial fisheries. The traject followed by the seabob fishery might serve as an example, guiding other fisheries in their improvements. Even though MSC certification might not be feasible or desired in other sectors of the Suriname fishery, the MSC standard can serve as a internal benchmark, or ultimate goal to achive. In any case, to apply an EAF, fisheries should make improvements related to (1) health of the exploited stock, (2) ecosystem impacts and (3) management. Three main priorities are defined to achieve this. First, major progress should be made in the collection, analysis and integration of data. The fishing sector should work together with the LVV fisheries ministry, and preferably also scientist and NGOs to get reliable information on the status of fish stocks and the wider ecosystem impact fishing activities. While data is currently being collected (including landings, VMS, and occasional data from sea-going observers), they are not being used for management purpuses, and stock assessments are currently only done for the seabob stock. Further, landing data should be complemented with information on bycatch, discards and ecosystem impacts. With more and reliable information becoming available, a second priority is to establish stakeholder meetings for every fishery. In analogy with the SWG, these meetings should serve as a platform to decide on management measures, based on reliable information. Finally, there is a clear need for more capacity of staff trained in fisheries science and management in Suriname.

4 FUTURE RESEARCH CHALLENGES AND OPPORTUNITIES

In several ways, this doctoral thesis sets a baseline for further ecosystem and fisheries research in Suriname. Through an extensive trawl survey (Chapters 2 and 3), we have provided updated information on the abiotic conditions and densities of epibenthic and demersal fish species on the inner Suriname Shelf. Further, we have revealed important aspects of the functioning of the coastal food web (Chapters 4 and 5), and provided information on the impact of seabob trawling on demersal assemblages (Chapters 6 and 7). Still, several challenges for future research stand out. As outlined above in section 2.2, the main priorities for future research are:

ECOSYSTEM MODELLING

Critical insights for fisheries management might be obtained through an overall ecosystem model for the coastal Suriname ecosystem. Most commonly this is done with the trophic mass-balance model Ecopath with Ecosim (EwE; e.g. Vasconcellos et al., 1997; Christensen and Pauly, 2004). Basically, EwE models require estimates on the biomasses of different ecosystem components, the magnitude of trophic links between them, the increase of biomass through

reproduction and growth, and the removal of biomass by fisheries (Pauly et al., 2000). Through this doctoral study, much of the information is now available to make an EwE ecosystem model for the coastal food web of Suriname. EwE models constitute excellent tools to gain insight in the ecological impacts of fisheries on ecosystem functioning, the indirect interactions among fishing fleets, and to explore management options (e.g. Griffiths et al., 2013; Coll et al., 2013; Lassen et al., 2013). For example, the effect of different rates of exploitation of *X. kroyeri* on the biomass of other resources and their fisheries could be assessed, as well as the ecosystem consequences of different levels of bycatch reduction.

LIFE CYCLE AND STOCK DYNAMICS OF *X. KROYERI*

Very limited information is currently available on the life cycle of *X. kroyeri* along the northern coast of South America. Like most penaeid shrimp, the species is assumed to undertake in-offshore migrations during its life cycle (Dall et al., 1990). However, the use of different offshore and coastal habitats (e.g. mangroves) by different life stages, remains unknown. Further, while temporal dynamics in the abundance of *X. kroyeri* postlarvae have been observed (Torrez, 2015), the timing of spawning and recruitment to the fishery warrants further investigation. Finally, the influence of environmental factors on recruitment and subsequent fisheries yields are poorly understood. Insights in all these aspects will allow for a better understanding of the dynamics of the offshore adult stock of *X. kroyeri*, and allow for ecosystem-based management measures.

STOCK STRUCTURE OF *X. KROYERI*

'Suriname seabob' is currently treated as a single stock unit in the stock assessment, separate from the 'Guyana seabob' (CRFM, 2009). However, it doesn't seem unlikely to assume that the *X. kroyeri* stock off Suriname is to some degree shared with the neighboring countries. Further, recent insights from genetic studies have shown that *X. kroyeri* might constitute of several (cryptic) species (e.g. Gusmao et al., 2013). The status of *X. kroyeri* in the Guianan Ecoregion, both in terms of population structure and genetics remains to be assessed.

Two main opportunities currently exist under which research outlined above might be executed. First, as of October 2015, a new PhD research started in collaboration with Ghent University, ILVO, KU Leuven and ADEK University of Suriname. This PhD study has the objectives to:

- *Investigate species and population structure of* X. kroyeri *in the Guianan Ecoregion;*
- *Study the life cycle of* X. kroyeri *in the coastal habitats of Suriname, with special emphasis on mangroves; and*

- *Study the feeding ecology of* X. kroyeri *in intertidal mangroves in relation to anthropogenic pressure.*

Second, the FAO project 'Sustainable management of Bycatch in Latin America and Caribbean Trawl Fisheries' (REBYC-II LAC) will run for the period 2015-2020, and will also include activities in Suriname. The objective of the REBYC-II LAC project in Suriname is *to improve the institutional and regulatory arrangement for shrimp/bottom trawl fisheries and bycatch co-management within an ecosystem approach to fisheries (EAF) management framework, strengthen bycatch management and reduce discards with responsible trawling practices within an EAF framework and promote sustainable and equitable livelihoods through enhancement and diversification of the bycatch value chain (FAO, 2016b).*

5 CONCLUSION

Under impulse of the MSC eco-labelling scheme, the Suriname seabob fishery has taken important steps towards the implementation of an Ecosystem Approach to Fisheries (EAF). The research in this thesis has addressed knowledge gaps related to the main aspects which an EAF should take into account. Based on the newly obtained information, the general validity of most measures taken so far in the Suriname seabob fishery is confirmed. Further, the research led to additional management recommendations related to (1) the spatio-temporal operation of the fishery, (2) fishing effort control and (3) gear-related aspects of the fishery. We also emphasize the crucial role of the Seabob Working Group as a stakeholder's platform to seek consensus on the management measures to be taken, and to keep track of their implementation. While the seabob fishery in Suriname can serve as an example of a well-managed fishery, the management of other fishing fleets will have to be reconsidered as well, in order to fully implement an EAF.

Whereas uncertainties remain, this thesis brought new insights on the structure and functioning of the coastal ecosystem supporting seabob fisheries off the coast of Suriname. This information was translated to fisheries management recommendations, by applying a precautionary approach. Through 'learning by doing', fisheries management should also embrace an adaptive approach, support further research, and make use of the best available knowledge. By applying these basic EAF principles, the Suriname seabob fishery can continue on the path of sustainable resource management.

The application of an EAF is often perceived as a complex and nearly impossible task. The trajectory of the Suriname seabob fishery shows that we should not see this process as a revolution, but rather as an evolution, in which continuous improvement is pursued. Participatory management, availability of reliable information and supporting ecosystem research is key to this process.

The Suriname seabob fishery shows that ecolabelling might have a catalytic role in the application on an EAF. The MSC-label was an important milstone in the path to sustainability of the Suriname seabob fishery, but further improvements are possible. The results of this doctoral thesis can form a scientific basis for these improvements.

ANNEX 1.1


Common marine invertebrates of the Guianas
Algemene mariene ongewervelden van de Guianas — Invertébrés marins communs des Guyanes
Turritella variegata
Conus compressus
Distorsio clathrata
Amygdalum politum
Trachycardium isocardia
Argopecten nucleus
Modiolus squamosus
Euvola chazaliei
Luidia clathrata
Renilla muelleri
Natica canrena
Dallocardia muricatum
Aequipecten linealaris
Ophiolepis elegans
Marisupina bulla
Fusinus anisatus
Terebra taurina
Ophioderma appressa
Luidia senegalensis
Murex pomum
Astrophyton muricatum
Echinoplysmata oplophoroides
Astropecten americanus
Loliguncula brevis
Doryteuthis plei
Penaeus subtilis
Nematopalaemon schmitti
Doryteuthis surinamensis
Hepatus acuper
Calappa nitida
Clibanarius forest
Xiphopenaeus kroyeri
Hepatus pudibundus
Petrochirus diogenes
Porcellana sayana
Hepatus gronovi
Calappa sulcata
Squilla empusa
Hypoconcha arcuata
Paradasygyius tuberculatus
Callinectes bocourti
Lupella forceps
Portunus spinimana
Portunus gibbesii
Persephona lichtensteinii
Callinectes ornatus
•This poster shows species commonly caught in the Guianas' coastal waters up to 40 m depth
•Design and layout ©Hans Hillewaert/ILVO
•Photographs ©Hans Hillewaert, Jan Ranson & Tomas Willems/ILVO
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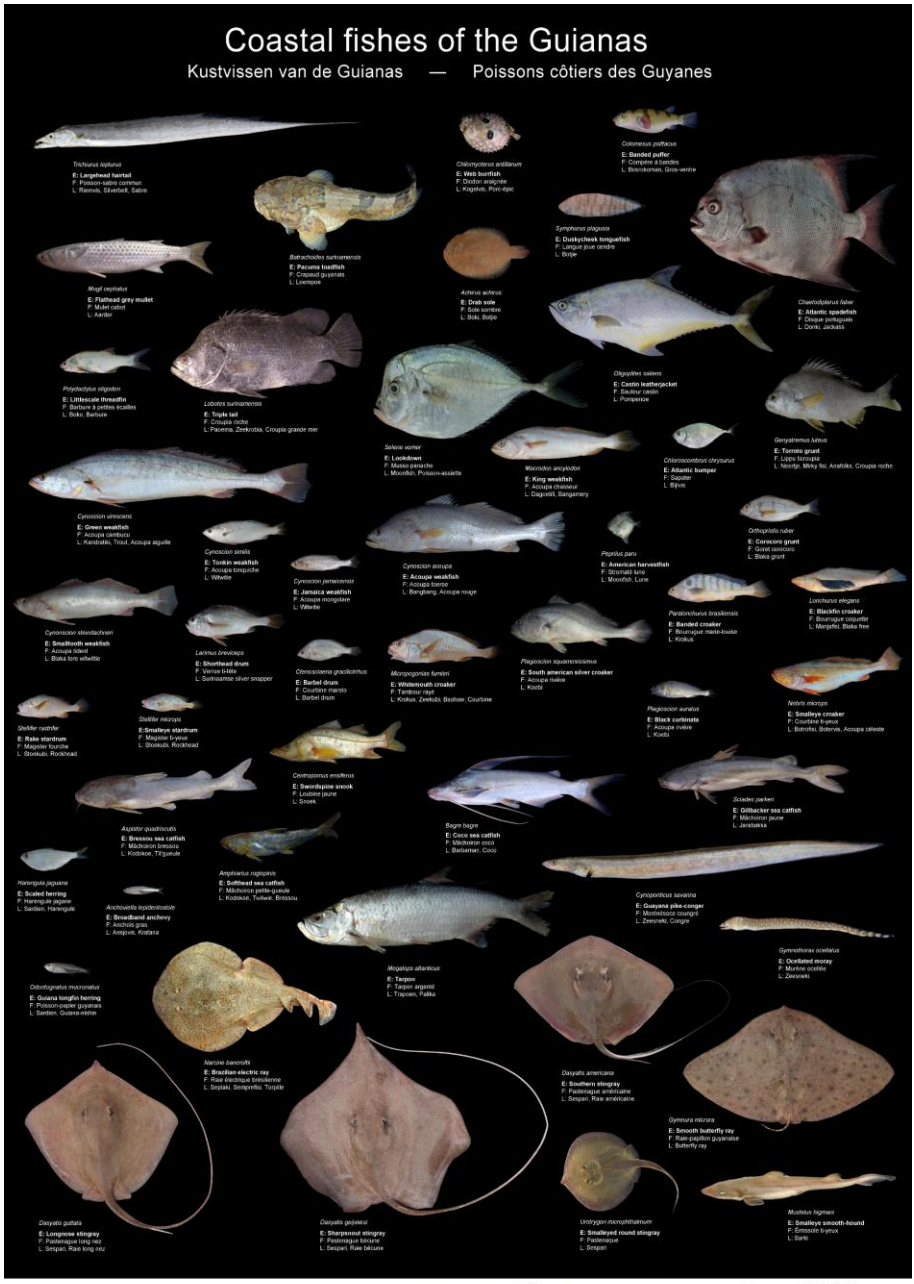
ANNEX 1.2


Coastal fishes of the Guianas
Kustvissen van de Guianas — Poissons côtiers des Guyanes
Trichiurus lepturus
E: Largehead hairtail
F: Poisson-sabre commun
L: Riemvis, Silverbelt, Sabre
Chilomycterus antillarum
E: Web burrfish
F: Diodon antillais
L: Kogelvis, Porc-épic
Colomesus psittacus
E: Banded puffer
F: Compère à bandes
L: Bronzekoman, Gros-ventre
Batrachoides surinamensis
E: Pacuma toadfish
F: Crapaud guyanais
L: Loempoe
Sympharus plagusia
E: Duskytoneh tonguefish
F: Langue joue cendre
L: Botje
Mugil cephalus
E: Flathead grey mullet
F: Mulet cabot
L: Aardar
Achirus achirus
E: Drab sole
F: Sole sombre
L: Boki, Botje
Chaetodipterus faber
E: Atlantic spadefish
F: Disque portugais
L: Donki, Jackass
Polydactylus oligodon
E: Littlescale threadfin
F: Barbure à petites écailles
L: Boko, Barbure
Lobotes surinamensis
E: Triple tail
F: Croupia roche
L: Pacema, Zeekrobia, Croupia grande mer
Oligoplites saliens
E: Castin leatherjacket
F: Blaikiur castin
L: Pompenoe
Selene vomer
E: Lookdown
F: Musso panaché
L: Moodfish, Poisson-assiette
Caranx latus
E: King weakfish
F: Acoupa chasseur
L: Dagveldi, Bangamary
Chloroscombrus chrysurus
E: Atlantic bumper
F: Sapatier
L: Bijlvis
Genyatremus luteus
E: Torroto grunt
F: Lippu torroupia
L: Neontje, Milky lips, Anafoliko, Croupia roche
Cynoscion virescens
E: Green weakfish
F: Acoupa vandoutu
L: Kandrafki, Trout, Acoupa aiguille
Cynoscion similis
E: Tookin weakfish
F: Acoupa tonquiche
L: Witvlte
Cynoscion jamaicensis
E: Jamaica weakfish
F: Acoupa mongolare
L: Witvlte
Cynoscion acoupa
E: Acoupa weakfish
F: Acoupa tonno
L: Bangtweg, Acoupa rouge
Pogrites parai
E: American harvestfish
F: Bromati lune
L: Moonfish, Lune
Orthopristis ruber
E: Corocoro grunt
F: Gront, corocoro
L: Blaka grunt
Cynoscion steindachneri
E: Smalltooth weakfish
F: Acoupa lobeli
L: Blaka toro witvlte
Larimus breviceps
E: Shorthead drum
F: Varrise à tête
L: Suriname silver snapper
Ctenosciaena gracilicirrhus
E: Barbel drum
F: Courbinto manto
L: Barbel drum
Menticirrhus littoralis
E: Gulf kingcroaker
F: Whiting du golfe
L: Golfwitvis
Paralonchurus brasiliensis
E: Banded croaker
F: Bourrugue maria-luisita
L: Krokus
Plagioscion squamosissimus
E: South american silver croaker
F: Acoupa rivière
L: Koebi
Plagioscion auratus
E: Black curbinata
F: Acoupa noire
L: Koebi
Nebris microps
E: Smalleye croaker
F: Courbine fe-yeux
L: Botnofisi, Botervis, Acoupa câlesté
Loncholurus elegans
E: Blackfin croaker
F: Bourrugue usquette
L: Margetfisi, Blake fins
Stellifer rastrifer
E: Rake stardrum
F: Magister tourcilier
L: Stonkudu, Rockhead
Stellifer microps
E:Smalleye stardrum
F: Magister fe-yeux
L: Stonkudu, Rockhead
Centropomus ensiferus
E: Swordspine snook
F: Loubine jaune
L: Snoek
Sciades parkeri
E: Gillbacker sea catfish
F: Mâchoiron jaune
L: Jansitakka
Aspistor quadriscutis
E: Bressou sea catfish
F: Mâchoiron bressou
L: Kodokoe, Tit'gueule
Bagre bagre
E: Coco sea catfish
F: Mâchoiron coco
L: Barbarman, Coco
Harengula jaguana
E: Scaled herring
F: Harengule jagane
L: Sardien, Harengule
Anchovella lepidentostole
E: Broadband anchovy
F: Anchois gras
L: Arejovis, Krafana
Amphiarius rugispinis
E: Softhead sea catfish
F: Mâchoiron petite-gueule
L: Kodokoe, Tuilwis, Brassou
Cynoponticus savanna
E: Guayana pike-conger
F: Murénoïdoce ouangni
L: Zeesneki, Congre
Gymnothorax ocellatus
E: Ocellated moray
F: Murène ocellée
L: Zeesneki
Odontognathus mucronatus
E: Guiana longfin herring
F: Poisson-papier guyanais
L: Sardien, Guiana-visnin
Megalops atlanticus
E: Tarpon
F: Tarpon argenté
L: Trapoen, Patiku
Narcine baancrofti
E: Brazilian electric ray
F: Raie électrique brésilienne
L: Seplaki, Sempreitsi, Torpille
Dasyatis americana
E: Southern stingray
F: Pastenague américaine
L: Sespari, Raie américaine
Gymnura micrura
E: Smooth butterfly ray
F: Raie-papillon guyanaise
L: Butterfly ray
Dasyatis guttata
E: Longnose stingray
F: Pastenague long nez
L: Sespari, Raie long nez
Dasyatis geijskesi
E: Sharpsnout stingray
F: Pastenague bécune
L: Sespari, Raie bécune
Urotrygon monophthalmum
E: Smalleyed round stingray
F: Pastenaque
L: Sespari
Mustelus higmani
E: Smalleye smooth-hound
F: Emissole fe-yeux
L: Siarki
•This poster shows 90 species commonly caught in the Guianas' coastal waters up to 30 m depth
•Fishes are printed to scale, representing the size at which they are commonly caught or marketed
•Scientific names are accompanied by, English (E), French (F) and local (L) names
•Design and layout ©Hans Hillewaert/ILVO, pictures ©Tomas Willems/ILVO
0 cm 5 cm 10 cm 20 cm
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ANNEX 1.3

Research on seabob trawl fishery Suriname

Sample collection at sea: Manual for captain, crew and LVV observers

In cooperation with:

ILVO

Marine Biology Ghent University

Anton de Kom Universiteit van Suriname
a higher degree, a higher purpose

Heiploeg Suriname

MINISTERIE VAN LANDBOUW, VEETEELT EN VISSERIJ

LVV

Research on seabob trawl fishery Suriname

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Introduction
Research is currently taking place on the trawl fishery for Atlantic seabob (*Xiphopenaeus kroyeri*) in Surinam, in order to comply with conditions set following MSC eco-labeling of this fishery in November 2011. Fieldwork for the research started in February 2012 and aims to collect information (1) to study seabed habitats and biological communities and (2) to assess the position of seabob in the foodweb.

Timing
To study seasonal fluctuations, sample collection will be done during **one whole year**. From February till July 2012 sampling will be done monthly switching to a 2-montly regime until January 2013. As such, after July 2012, sampling will need to done in **September 2012, November 2012 and January 2013** each time at the **end of the month** (after the 20th day of the month). Each research trip requires three full days of sampling work.

Logistics
The sampling is supported by the seabob company **Heiploeg Suriname** who provide a vessel for sample collection. The seabob trawler **Neptune-6** has all necessary equipment installed for taking and preserving samples, and its usual crew is trained for sample collection.

Locations
Sampling is done at **15 different locations** (stations) organized in 5 transects perpendicular to the coast in front of the river mouths of Coppename river **('Co-' samples)**, Suriname river **('Su-' samples)** and Marowijne river **('Ma-' samples)**, in a depth gradient from inshore to offshore. A map of sampling locations and their coordinates are provided in annexes 1 and 2.

Short description of the sampling
Sampling consists of **2 main parts**: (1) collecting a **sample of the fauna** inhabiting the seabed and (2) gathering **information on the environment**. Seabed fauna is sampled using a small bottom trawl (try-net) for 40 minutes. The catch is separated in fish, seabob and invertebrates. Next to that, a CTD is deployed to measure water parameters, a water sample is taken with a Niskin-bottle and a Secchi disk is used to assess water clarity.

ANNEX 1.3 continued.

Sample collection at sea: Manual for captain, crew and LVV observers

STEP-BY-STEP sampling manual

➔ **To be repeated at each station (15 times)**

➔ **See Annex 1 and 2 for sampling locations and coordinates**

Overview

1/ Arrival at the correct location

2/ Try-net overboard (speed 2-4 knots)

3/ Haul try-net (boat stops)

5/ Take profile with the CTD

6/ Take a water sample with the Niskin bottle

7/ Measure water clarity with Secchi disk

8/ Process the try-net catch (boat can move on)

ANNEX 1.3 **continued.**

1. Arrival at the correct location

➔ **Fill in** sample form:

- Date
- Time
- Station
- Depth (in feet)
- Rain
- Wind

2. Try-net overboard

➔ Take the **GPS position** and **time** the net is set overboard

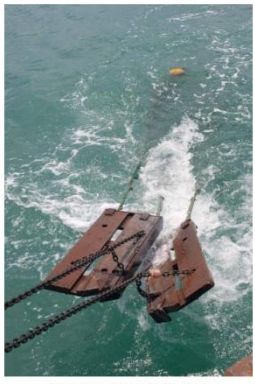
➔ Drag in **eastwards direction**

3. Haul try-net (boat stops)

➔ Haul the net after **40 minutes**

➔ Take the **GPS position** and **time** the net is brought up

➔ Bring the catch on deck in a basket and put aside



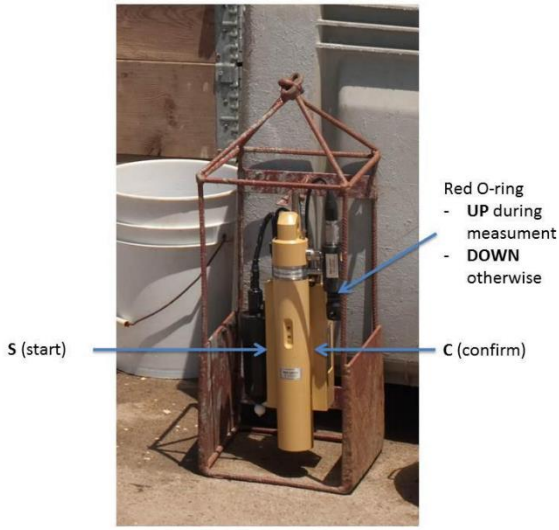
The try-net coming up

4. Take CTD-profile

A CTD measures Conductivity (= salinity), Temperature, and Depth of the water. These parameters should be measured in the whole water column, so the CTD should go **to the bottom** before bringing it up again.

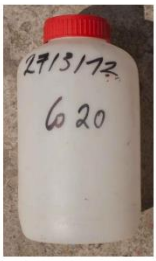
Making a CTD measurement:

- ➔ Bring the red **O-ring** in **upper** position
- ➔ **Start** the device: with the magnetic key, slowly slide of the **S-strip**, and **than** over the **C-strip**
- ➔ The device is working when the **red C-lamp blinks** every 5 seconds
- ➔ Put the CTD in the water and **wait for 1 minute** to callibrate
- ➔ Lower the CTD to the seabottom and bring it back up
- ➔ **Stop** the device: with the magnetic key, slowly slide of the **C-strip**, and **than** over the **S-strip**
- ➔ Make shure **no lights are blinking**
- ➔ Bring the red O-ring in **lower** position
- ➔ Rince the device with some **fresh water** after use



5. Take a water sample with Niskin bottle

➔ **Label** a plastic 2L bottle with **date and station**
➔ Tight the lids of the bottle correctly before putting it overboard
➔ Lower the bottle to 5m depth
➔ Close it using the messenger and bring back on deck
➔ Transfer a water sample into a plastic 2L bottle, close it well!
➔ Store the sample in the **freezer**



6. Measure water visibility with Secchi disk

- ➔ Lower the Secchi disk in the water
- ➔ Using the scale markings on the rope, note the depth **when the disk just becomes invisible** (0,2m precise)
- ➔ **Note this depth at the form (=Secchi-depth)**

Secchi disk with markings each 0,2 m (red-yellow) and 1m (black) interval

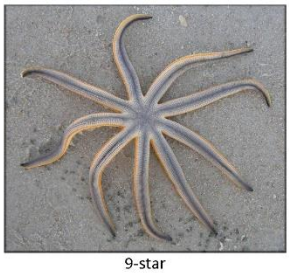
7. Sort try-net catch (boat can move on)

➔ **Separate invertebrates, fish and seabob**

A. INVERTEBRATES (crabs, sea stars, prawns, hermit crabs, shells,...)

➔ Label a plastic bag with **date and station**
➔ Put all invertebrates together in the bag
➔ Store the bag in the **freezer**

➔ The following organisms -when very numerous- can be counted, **noted** on the form and **discarded**: '9-star' and 'sea-ear'


9-star


Sea-ear

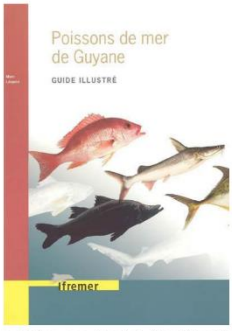
➔ **Jellyfish** are never taken: **count and note** on form as 'Jelly'

B. FISH

- ➔ Identify all fish to species level (See Annex 3)
- ➔ For **rays**: measure **body width** (1 cm precision) and determine **sex**
- ➔ For all other **fish**: measure **body length** (1 cm precision)
- ➔ Note all measurement on the form
- ➔ After measurement, all fish can be **discarded**

- ➔ **Fishes which are labeled with 'TO PRESERVE' in Annex 3 should be stored in the freezer, together with the invertebrates**
- ➔ **Other (small) fishes which are difficult to identify are also taken in the freezer, together with the invertebrates.**

These rulers, together with a measuring tape, are used to measure the fish



When doubting, use the fish identification guide

C. SEABOB

- ➔ **Label** a plastic bag with **date and station**
- ➔ Check carefully if **no** (juvenile) **prawns** are between the seabob. These should be stored together with the invertebrates
- ➔ Using the graduated bucket, determine the **total volume of seabob** (in liters) in the trynet catch
- ➔ **Note the total volume** of seabob on the form
- ➔ Using the graduated cylinder, take a subsample of **one liter of seabob**
- ➔ Transfer one liter of seabob to the labeled plastic bag and store in the **freezer**

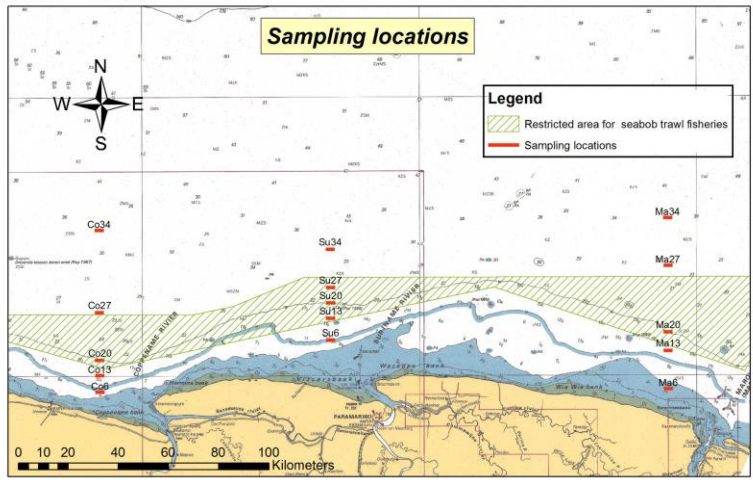
- ➔ If no seabob was caught, note **'No seabob'** on the form
- ➔ If **less than one liter** of seabob was caught, transfer **all seabob** to a labeled plastic bag and store in the freezer

Graduated bucket to determine **volume of seabob**

Graduated cylinder to take **1L subsample**

ANNEX 1.3 continued.

ANNEX 1. Map of sampling locations



ANNEX 2: Coordinates of sampling locations (stations)

Start points of try-net fishtracks

Co34	6	31	32.729	N	56	10	7.993	W
Co27	6	13	43.982	N	56	10	7.892	W
Co20	6	3	24.329	N	56	10	6.751	W
Co13	6	0	8.312	N	56	10	4.688	W
Co6	5	57	35.014	N	56	10	3.428	W

Su34	6	27	20.974	N	55	20	11.357	W
Su27	6	19	4.44	N	55	20	8.279	W
Su20	6	15	43.196	N	55	20	8.261	W
Su13	6	12	24.289	N	55	20	8.603	W
Su6	6	7	41.668	N	55	20	7.771	W

Ma34	6	33	52.805	N	54	7	7.262	W
Ma27	6	23	32.644	N	54	7	5.768	W
Ma20	6	9	11.804	N	54	7	11.266	W
Ma13	6	5	8.063	N	54	7	11.636	W
Ma6	5	56	54.298	N	54	7	11.633	W

ANNEX 2.1 **Average (± SD) values of water and sediment parameters per depth, transect and season and results of three-way Permanova tests on Euclidean distance resemblance matrices with the factors 'depth', 'transect' and 'season'. CHL=remote sensing chlorophyll a values (in mg.m-3); SS-TSM=in situ measured sub-surface total suspended matter (in g.m-3); SF-TSM=remote sensing surface total suspended matter (in g.m-3); SST=remote sensing sea surface temperature (in °C); SECCHI=in situ measured Secchi-depth (in m); TOC=total organic carbon content (in %); MEDSAND=median grain size of sand fraction (in μm); MUD=sediment mud content (in %); (the latter three derived from in situ bottom-grab samples).**

Variable	Depth					Transect			Season		Main test		
	6	13	20	27	34	Co	Su	Ma	Dry	Rainy	Significant term	Pseudo-F	P
CHL	**5.2 ± 2.1**	**4.1 ± 1.6**	**3.4 ± 1.5**	**2.4 ± 1.2**	**1.6 ± 1.4**	**3.3 ± 2.2**	**3.2 ± 2.3**	**3.5 ± 1.4**	**3.0 ± 1.7**	**3.7 ± 2.2**	**depth**	**24.2**	**0.0001**
											season	**7.9**	**0.0056**
Pairwise tests		*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
		depth	depth	-	6, 13	2.3	0.023	depth	depth	-	13, 34	6.4	0.0001
		depth	depth	-	6, 20	3.9	0.0002	depth	depth	-	20, 27	2.9	0.0045
		depth	depth	-	6, 27	6.5	0.0001	depth	depth	-	20, 34	4.8	0.0001
		depth	depth	-	6, 34	7.7	0.0001	depth	depth	-	27, 34	2.6	0.0122
		depth	depth	-	13, 27	4.8	0.0001						
SS-TSM	**99.0 ± 53.7**	**50.6 ± 17.7**	**43.9 ± 15.3**	**39.2 ± 14.4**	**36.0 ± 11.3**	**57.4 ± 41.3**	**47.1 ± 26.4**	**56.4 ± 36.9**	**46.5 ± 32.9**	**60.6 ± 36.7**	**depth**	**27.9**	**0.0001**
											season	**8.6**	**0.0035**
Pairwise tests		*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
		depth	depth	-	6, 13	4.9	0.0001	depth	depth	-	13, 27	2.8	0.0074
		depth	depth	-	6, 20	5.6	0.0001	depth	depth	-	13, 34	3.7	0.0003
		depth	depth	-	6, 27	6.1	0.0001	depth	depth	-	20, 34	2.1	0.0396
		depth	depth	-	6, 34	6.4	0.0001						
SF-TSM	**11.6 ± 4.1**	**6.8 ± 3.7**	**4.5 ± 3.1**	**2.4 ± 1.5**	**1.1 ± 1.0**	**4.3 ± 4.6**	**4.6 ± 3.9**	**6.9 ± 5.1**	**5.5 ± 4.9**	**5.1 ± 4.5**	**depth x transect**	**2.2**	**0.0301**
Pairwise tests		*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
		depth x transect	transect	Co	6, 13	2.4	0.0305	depth x transect	transect	Ma	13, 34	4.6	0.0007
		depth x transect	transect	Co	6, 20	5.7	0.0001	depth x transect	transect	Su	6, 20	2.9	0.0117
		depth x transect	transect	Co	6, 27	6.6	0.0001	depth x transect	transect	Su	6, 27	6.1	0.0002
		depth x transect	transect	Co	6, 34	8.4	0.0001	depth x transect	transect	Su	6, 34	7.7	0.0001

ANNEX 2.1 continued.

Variable	Depth					Transect			Season		Main test		
	6	13	20	27	34	Co	Su	Ma	Dry	Rainy	Significant term	Pseudo-F	P
		depth x transect	transect	Co	13, 27	4.1	0.0007	depth x transect	transect	Su	13, 34	5.6	0.0001
		depth x transect	transect	Co	13, 34	6	0.0001	depth x transect	transect	Su	20, 27	3.3	0.0045
		depth x transect	transect	Co	20, 34	5.3	0.0002	depth x transect	transect	Su	20, 34	5.4	0.0002
		depth x transect	transect	Co	27, 34	3.3	0.003	depth x transect	transect	Su	27, 34	5.1	0.0005
		depth x transect	transect	Ma	6, 13	5.1	0.0003	depth x transect	depth	13	Ma, Su	3.1226	0.0059
		depth x transect	transect	Ma	6, 20	6.5	0.0001	depth x transect	depth	20	Co, Su	3.4361	0.0049
		depth x transect	transect	Ma	6, 27	7.8	0.0001	depth x transect	depth	20	Ma, Su	3.9131	0.0017
		depth x transect	transect	Ma	6, 34	7.4	0.0001	depth x transect	depth	27	Co, Su	2.2888	0.0387
		depth x transect	transect	Ma	13, 20	2.4	0.0273	depth x transect	depth	27	Ma, Su	4.6121	0.0005
		depth x transect	transect	Ma	13, 27	4.7	0.0002						
SST	**28.7 ± 1.2**	**28.1 ± 1.1**	**27.9 ± 1.0**	**27.8 ± 1.0**	**27.8 ± 1.1**	**27.9 ± 1.0**	**28.2 ± 1.1**	**28.0 ± 1.2**	**28.3 ± 1.2**	**27.9 ± 1.0**	**depth season**	**3.1 4.1**	**0.0188 0.0443**
Pairwise tests		*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
		depth	depth	-	6, 20	2.4	0.0191	depth	depth		6, 34	2.8	0.0081
		depth	depth		6, 27	2.9	0.0056						
SECCHI	**0.8 ± 0.5**	**1.7 ± 1.0**	**2.9 ± 1.4**	**4.7 ± 2.1**	**8.3 ± 3.3**	**4.8 ± 3.7**	**3.7 ± 3.2**	**2.6 ± 2.5**	**3.7 ± 3.4**	**3.6 ± 3.1**	**depth x transect**	**3.5**	**0.001**
Pairwise tests		*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
		depth x transect	transect	Co	6, 20	3.1	0.0064	depth x transect	transect	Su	6, 13	4.3	0.0008
		depth x transect	transect	Co	6, 27	5.9	0.0002	depth x transect	transect	Su	6, 20	6.6	0.0002

ANNEX 2.1 continued.

Variable	Depth					Transect			Season		Main test		
	6	13	20	27	34	Co	Su	Ma	Dry	Rainy	Significant term	Pseudo-F	P
		depth x transect	transect	Co	13, 27	4.5	0.0006	depth x transect	transect	Su	6, 34	4.6	0.0001
		depth x transect	transect	Co	13, 34	7.2	0.0001	depth x transect	transect	Su	13, 20	3.3	0.0026
		depth x transect	transect	Co	20, 34	5.8	0.0002	depth x transect	transect	Su	13, 27	5.8	0.0001
		depth x transect	transect	Co	27, 34	4.6	0.0005	depth x transect	transect	Su	13, 34	4	0.0005
		depth x transect	transect	Ma	6, 13	3.4	0.002	depth x transect	transect	Su	20, 27	2.7	0.014
		depth x transect	transect	Ma	6, 20	5.9	0.0002	depth x transect	transect	Su	20, 34	3.2	0.0007
		depth x transect	transect	Ma	6, 27	13.8	0.0001	depth x transect	transect	Su	27, 34	2.3	0.0157
		depth x transect	transect	Ma	6, 34	16.3	0.0001	depth x transect	depth	6	Co, Ma	2.1465	0.049
		depth x transect	transect	Ma	13, 20	2.5	0.0234	depth x transect	depth	6	Co, Su	3.0192	0.005
		depth x transect	transect	Ma	13, 27	7.9	0.0001	depth x transect	depth	13	Ma, Su	2.1757	0.024
		depth x transect	transect	Ma	13, 34	11.4	0.0001	depth x transect	depth	20	Ma, Su	3.0128	0.004
		depth x transect	transect	Ma	20, 27	4.7	0.0009	depth x transect	depth	27	Co, Ma	4.7325	0.002
		depth x transect	transect	Ma	20, 34	8.4	0.0002	depth x transect	depth	27	Ma, Su	7.1323	0.001
		depth x transect	transect	Ma	27, 34	4.8	0.0002	depth x transect	depth	34	Ma, Su	3.154	0.009
MEDSAND	**90.8 ± 1.8**	**127.8 ± 56.8**	**137.4 ± 58.7**	**189.8 ± 24.3**	**318.1 ± 105.8**	**183.5 ± 48.8**	**151.7 ± 75.0**	**182.3 ± 144.2**	**173.3 ± 99.1**	**171.4 ± 99.4**	**depth**	**6**	**0.006**

Pairwise tests	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
	depth	depth	-	6, 27	19.7	0.0001	depth	depth	-	13, 34	2.6	0.0399
	depth	depth	-	6, 34	3.9	0.0109	depth	depth	-	20, 34	2.6	0.0339

ANNEX 2.1 continued.

Variable	Depth					Transect			Season		Main test		
	6	13	20	27	34	Co	Su	Ma	Dry	Rainy	Significant term	Pseudo-F	P
Pairwise tests		*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
		depth	depth	-	6, 27	11.9	0.0002	depth	depth	-	13, 34	5.5	0.0034
		depth	depth	-	6, 34	5.5	0.0032	depth	depth	-	20, 27	5.4	0.0019
		depth	depth	-	13, 27	12	0.0001	depth	depth	-	20, 34	4.3	0.0049
TOC	**1.2 ± 0.2**	**1.1 ± 0.1**	**1.0 ± 0.1**	**0.6 ± 0.3**	**0.4 ± 0.0**	**0.8 ± 0.4**	**0.8 ± 0.3**	**0.9 ± 0.3**	**0.9 ± 0.3**	**0.9 ± 0.3**	**depth x transect**	**4.4**	**0.007**
Pairwise tests		*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*	*Significant term*	*Factor*	*Level*	*Groups tested*	*t*	*P*
		depth x transect	transect	Co	6, 27	14.9	0.0112	depth x transect	transect	Ma	13, 34	6.5	0.0226
		depth x transect	transect	Co	6, 34	15.7	0.0121	depth x transect	transect	Su	6, 34	12.7	0.0112
		depth x transect	transect	Co	13, 27	7.8	0.0189	depth x transect	transect	Su	13, 34	9.8	0.0108
		depth x transect	transect	Co	13, 34	8.6	0.0113	depth x transect	transect	Su	20, 34	12.1	0.0108
		depth x transect	transect	Co	20, 27	8.8	0.011	depth x transect	transect	Su	27, 34	7.3	0.0202
		depth x transect	transect	Co	20, 34	9.7	0.0113	depth x transect	depth	6	Co, Ma	7.1091	0.0251
		depth x transect	transect	Ma	6, 13	8.8	0.0095	depth x transect	depth	6	Ma, Su	5.8036	0.0341
		depth x transect	transect	Ma	6, 27	5.8	0.0235	depth x transect	depth	27	Co, Su	7.1151	0.0224

ANNEX 2.2a. Results from three-way Permanova analyses of species composition and abundance within clusters (assemblages) using factors 'depth', 'transect' and 'season'. The analysis was based on a Bray-Curtis similarity index constructed of fourth-root transformed epibenthos abundance data of the stations classified within a cluster. Only significant results (p<0.05) are shown.

Within-cluster pairwise tests of epibenthic species compostion and abundance						
Assemblage	Significant term	Factor	Level	Groups tested	t	P
Coastal	depth x transect	transect	Co	6, 20	1.8232	0.0135
Coastal	depth x transect	transect	Co	6, 27	2.1138	0.0148
Coastal	depth x transect	transect	Co	13, 27	1.697	0.0183
Coastal	depth x transect	transect	Ma	6, 27	2.188	0.0055
Coastal	depth x transect	transect	Ma	13, 27	2.6091	0.0009
Coastal	depth x transect	transect	Ma	20, 27	1.7222	0.024
Coastal	depth x transect	transect	Su	6, 13	1.8153	0.0093
Coastal	depth x transect	transect	Su	6, 20	1.9347	0.0018
Coastal	depth x transect	depth	6	Co, Ma	2.2564	0.0035
Coastal	depth x transect	depth	6	Co, Su	3.1732	0.0002
Coastal	depth x transect	depth	6	Ma, Su	2.6221	0.0002
Coastal	depth x transect	depth	13	Co, Ma	2.4978	0.0006
Coastal	depth x transect	depth	13	Ma, Su	1.8611	0.0157
Coastal	depth x transect	depth	20	Co, Ma	2.0637	0.0053
Coastal	depth x transect	depth	20	Ma, Su	2.1537	0.002
Coastal	depth x transect	depth	27	Ma, Su	1.62	0.0317
Transition	Transect	transect	-	Co, Ma	1.9024	0.0038
Transition	Transect	transect	-	Ma, Su	2.185	0.0008

ANNEX 2.2b. Results from three-way Permanova analyses of univariate parameters within clusters (assemblages) using factors 'depth', 'transect' and 'season'. The analysis was based on an Euclidean distance resemblance matrix of the stations classified within a cluster. Only significant results (p<0.05) are shown.

Within-cluster pairwise tests of univariate parameters							
Parameter	Assemblage	Significant term	Factor	Level	Groups tested	t	P
H'	Coastal	depth x transect	transect	Co	6, 27	4.0846	0.017
H'	Coastal	depth x transect	transect	Co	13, 27	3.1359	0.0137
H'	Coastal	depth x transect	transect	Su	6, 13	3.0132	0.0036
H'	Coastal	depth x transect	transect	Su	13, 20	2.7408	0.015
H'	Coastal	depth x transect	transect	Su	13, 27	3.8441	0.0021
H'	Coastal	depth x transect	depth	6	Ma, Su	2.6334	0.0195
H'	Coastal	depth x transect	depth	13	Co, Ma	2.7005	0.0136
H'	Coastal	depth x transect	depth	13	Co, Su	2.3157	0.0306
H'	Coastal	depth x transect	depth	27	Co, Su	22.196	0.0392
H'	Coastal	depth x transect	depth	27	Co, Ma	3.3046	0.0221
H'	Coastal	transect x season	season	rainy	Co, Ma	4.3618	0.0006
H'	Coastal	transect x season	season	rainy	Ma, Su	2.6654	0.0108
H'	Coastal	transect x season	transect	Co	dry, rainy	3.3433	0.006
J'	Coastal	Season	season	-	dry, rainy	2.234	0.0346
J'	Transition	Transect	transect	-	Co, Ma	2.2667	0.0403
J'	Transition	Transect	transect	-	Co, Su	2.3128	0.0407
J'	Transition	Transect	transect	-	Ma, Su	5.9968	0.0001
S	Coastal	Depth	depth	-	6, 13	2.3238	0.0244
S	Coastal	Depth	depth	-	6, 20	4.3931	0.0003
S	Coastal	Depth	depth	-	6, 27	5.2934	0.0002
S	Coastal	Depth	depth	-	13, 20	2.4913	0.0146
S	Coastal	Depth	depth	-	13, 27	3.4549	0.0016
S	Coastal	Transect	transect	-	Co, Ma	4.5813	0.0001
S	Coastal	Transect	transect	-	Co, Su	2.5691	0.0178
S	Coastal	Transect	transect	-	Ma, Su	2.4324	0.0176
S	Transition	Transect	transect	-	Co, Ma	2.6557	0.0208
S	Transition	Transect	transect	-	Ma, Su	3.4864	0.0052
B	Offshore	Transect	transect	-	Co, Su	2.4047	0.027

ANNEX 3.1. Community tests within assemblages. Only significant resulst (P<0.05) are given.

Within-assemblage pairwise tests of fish species composition and abundance						
Assemblage	Significant term	Factor	Level	Groups tested	t	P
coastal	depth x transect	transect	Co	6, 13	1.4567	0.0343
coastal	depth x transect	transect	Co	6, 20	2.6513	0.0001
coastal	depth x transect	transect	Co	6, 27	2.6331	0.0162
coastal	depth x transect	transect	Co	13, 27	1.8333	0.0166
coastal	depth x transect	transect	Ma	6, 13	1.8281	0.0001
coastal	depth x transect	transect	Ma	6, 20	1.5479	0.0038
coastal	depth x transect	transect	Ma	6, 27	2.531	0.0018
coastal	depth x transect	transect	Ma	13, 27	1.9883	0.0026
coastal	depth x transect	transect	Ma	20, 27	1.9798	0.0227
coastal	depth x transect	transect	Su	6, 13	1.8773	0.0013
coastal	depth x transect	transect	Su	6, 20	2.6438	0.0003
coastal	depth x transect	transect	Su	6, 27	2.2248	0.0027
coastal	depth x transect	transect	Su	13, 20	1.6987	0.0049
coastal	depth x transect	transect	Su	13, 27	1.5686	0.0238
coastal	depth x transect	depth	6	Co, Ma	2.4228	0.0001
coastal	depth x transect	depth	6	Co, Su	2.4872	0.0001
coastal	depth x transect	depth	6	Ma, Su	1.8643	0.0016
coastal	depth x transect	depth	13	Co, Ma	1.8293	0.0017
coastal	depth x transect	depth	20	Co, Ma	1.6832	0.0066
coastal	depth x transect	depth	20	Ma, Su	1.4008	0.0336
coastal	season	season	-	dry, rainy	1.4205	0.0376
offshore	season	season	-	dry, rainy	1.4165	0.0366

ANNEX 3.2. Univariate parameter tests within assemblages.

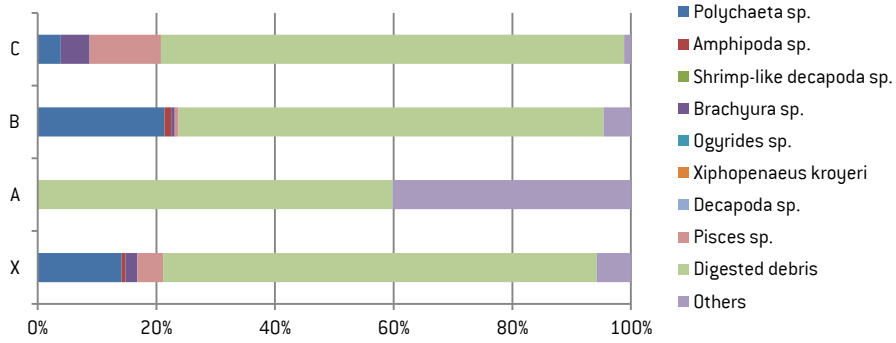
Within-assemblage pairwise tests of univariate parameters							
Parameter	Assemblage	Significant term	Factor	Level	Groups tested	t	P
S	coastal	depth	depth	-	6, 27	2.462	0.0194
S	coastal	depth	depth	-	13, 27	2.411	0.0199
S	coastal	transect x season	season	dry	Co, Ma	2.719	0.0127
S	coastal	transect x season	season	dry	Ma, Su	3.138	0.0048
N	coastal	depth	depth	-	6, 27	2.204	0.0421
N	coastal	depth	depth	-	13, 27	2.839	0.0113
N	coastal	depth	depth	-	20, 27	2.804	0.0106
N	coastal	transect	transect	-	Co, Ma	2.441	0.0273
N	coastal	transect	transect	-	Co, Su	2.424	0.0233
H'	coastal	depth x transect	transect	Co	20, 27	3.643	0.0133
H'	coastal	depth x transect	transect	Ma	13, 20	2.329	0.0406
H'	coastal	depth x transect	transect	Su	6, 13	2.209	0.0429
H'	coastal	depth x transect	transect	Su	6, 20	2.631	0.0194
S	offshore	season	season	-	dry, rainy	2.119	0.0469

ANNEX 5.1. **Gravimetrical diet composition (barplots) and list of prey types (tables) of 13 demersal fish species sampled off the coast of Suriname, based on stomach content analysis. n=number of analysed stomachs; E=number of empty stomachs.**

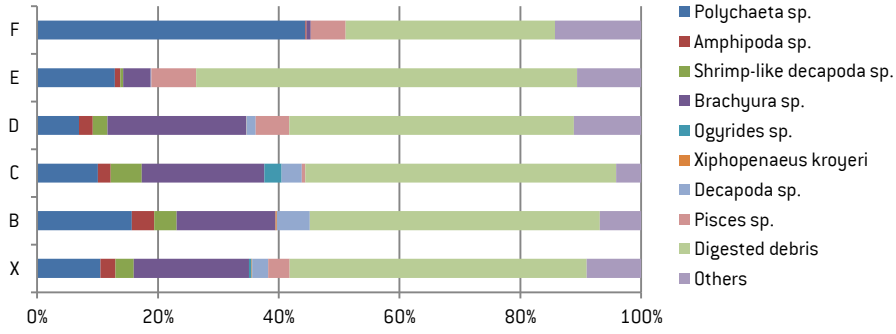
In the barblots, prey types were lumped to higher taxonomic level, and items with low gravimetrical contributions were grouped as 'others'. The diet is represented per 5 cm length-classes, and as overal diet (indicated as X). A=5-9cm, B=10-14cm, C=15-19cm, D=20-24cm, E=25-29cm, F=30-34cm, G=35-39cm, H=40-44cm, I=45-49cm, J=50-54cm, K=55-59cm, L=60-64cm, M=65-69cm, N=70-74cm, O=75-79cm, P=80-84cm

In the tables, the relative importance of each prey type is indicated with the frequency of occurrence (%FO), numerical (%N) and gravimetric (%G) abundance index and feeding coefficient (Q = %N x %G).

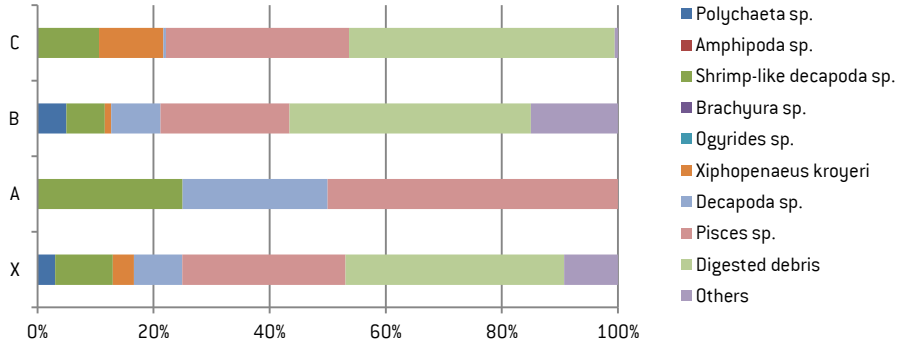
Achirus achirus (n=31; E=1)



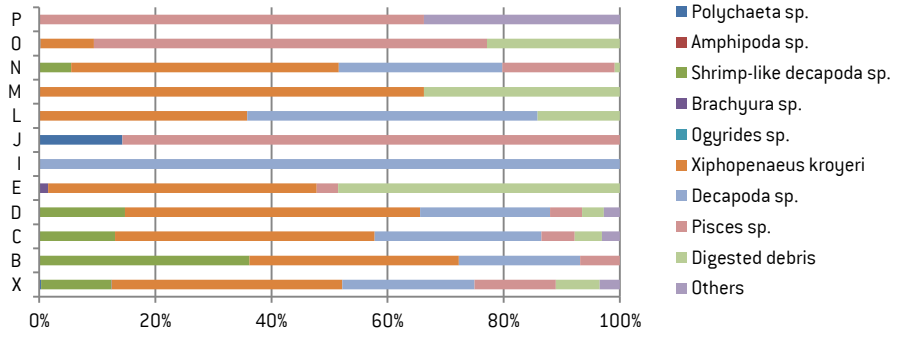
Amphiarius rugispinis (n=98; E=1)



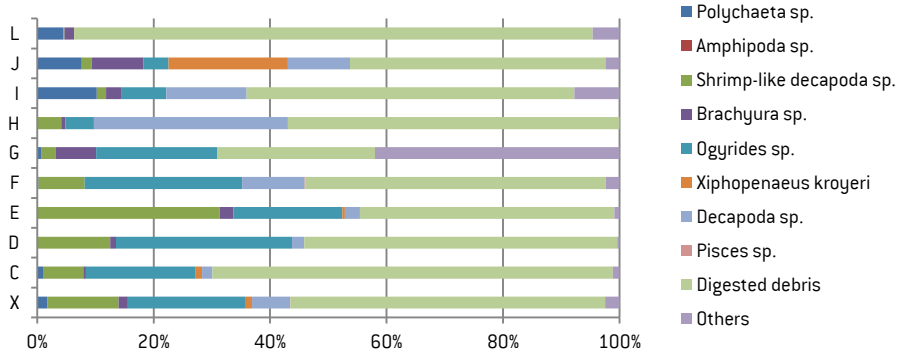
Cynoscion jamaicensis (n=33; E=0)



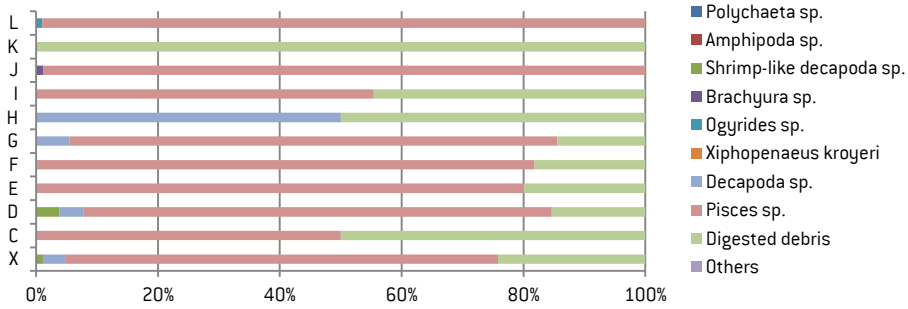
Cynoscion virescens (n=51; E=0)



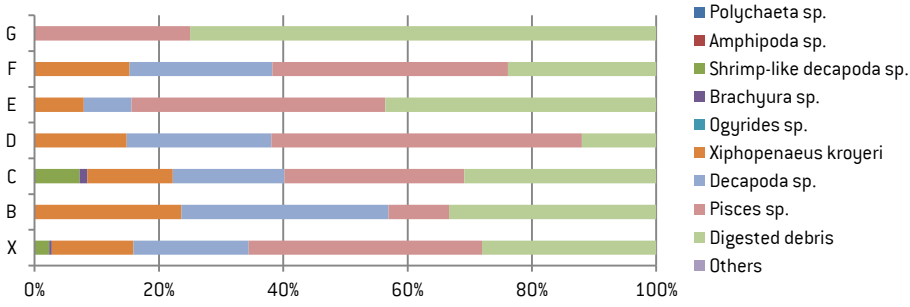
Dasyatis guttata (n=71; E=3)



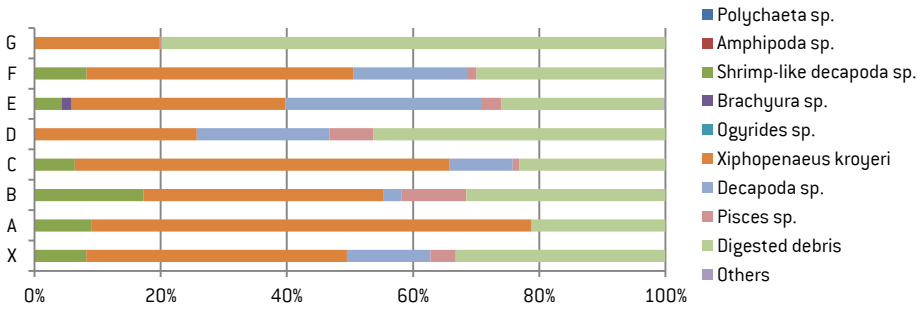
Gymnura micrura (n=65; E=17)



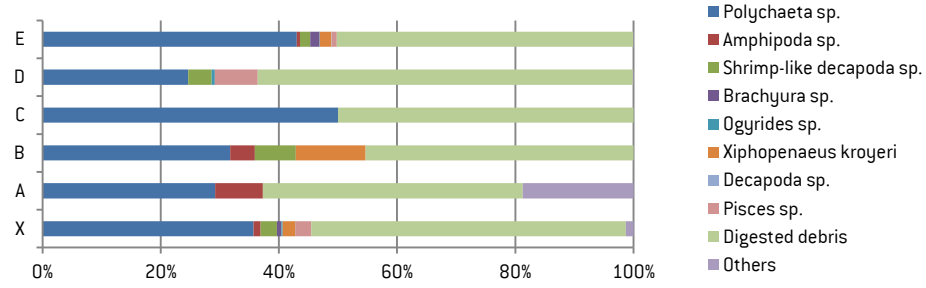
Macrodon ancylodon (n=92; E=1)



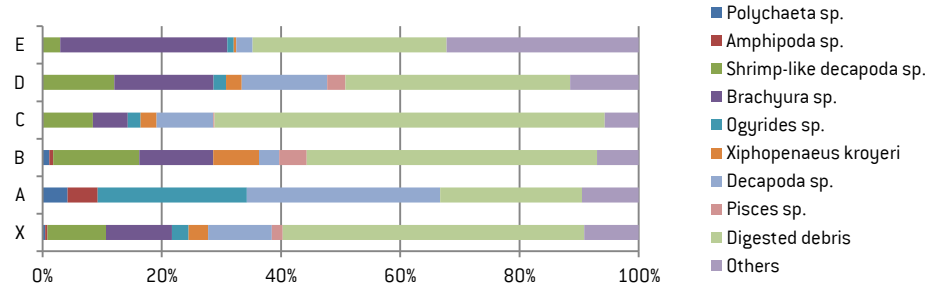
Nebris microps (n=66; E=1)



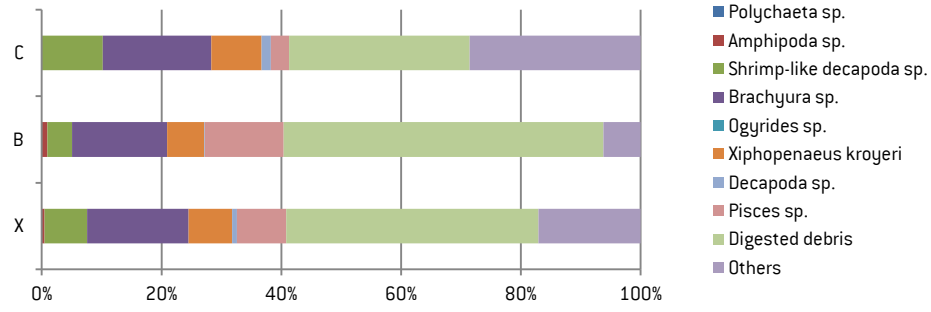
***Paralonchurus brasiliensis* (n=63; E=3)**



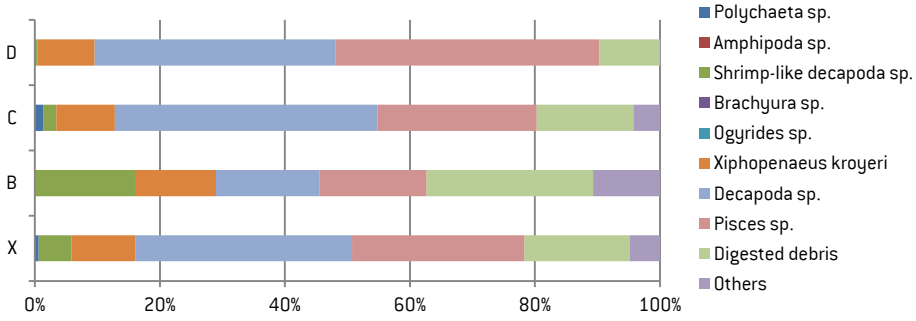
***Prionotus punctatus* (n=67; E=4)**



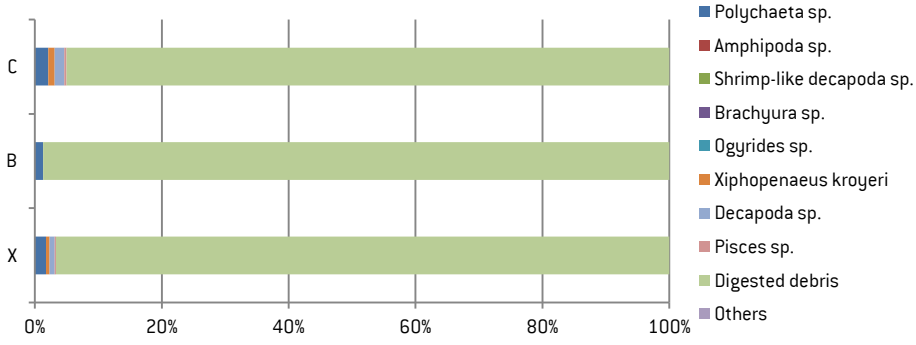
***Stellifer microps* (n=39; E=4)**



Stellifer rastrifer **(n=48; E=1)**



Symphurus plagusia **(n=32; E=1)**



Achirus achirus (n=31; E=1)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	30.0	25.4	17.2	437.2
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	3.3	4.5	0.2	0.9
Crustacea				
Unidentified sp.	3.3	4.5	5.9	26.2
Amphipoda				
Unidentified sp.	3.3	1.5	0.7	1.1
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp. postlarva	0.0	0.0	0.0	0.0
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	10.0	4.5	2.2	9.8
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	3.3	1.5	1.5	2.2
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	0.0	0.0	0.0	0.0
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	0.0	0.0	0.0	0.0
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	6.7	4.5	8.4	37.4
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	13.3	7.5	1.9	14.2
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	3.3	1.5	7.4	11.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	100.0	44.8	54.7	2450.2
Plastic fibres	0.0	0.0	0.0	0.0

Amphiarius rugispinis (n=98; E=1)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	13.4	2.7	2.1	5.7
Aonides sp.	16.5	8.9	2.5	22.4
Cirratulidae sp.	2.1	0.5	1.0	0.5
Platyhelminthes				
Platyhelminthes sp.	1.0	0.3	<0.1	<0.1
Crustacea				
Unidentified sp.	6.2	0.9	0.2	0.2
Amphipoda				
Unidentified sp.	51.5	28.6	2.8	81.4
Caprellidae sp.	1.0	0.1	<0.1	<0.1
Copepoda				
Unidentified sp.	4.1	1.1	6.6	7.1
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	15.5	2.6	0.6	1.7
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	11.3	1.9	1.6	3.0
Shrimp-like decapoda sp. postlarva	2.1	0.2	0.1	<0.1
Acetes americanus	4.1	0.6	0.4	0.2
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	1.0	0.1	0.1	<0.1
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	39.2	14.3	17.8	253.4
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	12.4	3.5	0.8	2.7
Calappidae sp.	3.1	12.6	0.5	6.3
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	1.0	0.1	<0.1	<0.1
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	0.0	0.0	0.0	0.0
Ogyrides sp.	1.0	0.2	0.4	0.1
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	1.0	0.1	0.1	<0.1
Penaeus brasiliensis	1.0	0.1	0.4	<0.1
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	0.0	0.0	0.0	0.0
X. kroyeri postlarve	2.1	0.4	<0.1	<0.1
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	2.1	0.2	<0.1	<0.1
Unidentified sp. larva	5.2	2.2	0.2	0.5
Squilla sp.	3.1	0.3	3.9	1.1
Squilla lijdingi	3.1	0.5	3.9	1.9
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	15.5	2.7	1.0	2.8
Mactridae sp.	1.0	0.1	0.1	<0.1
Nuculidae sp.	1.0	0.8	3.0	2.3
Pectinidae sp.	1.0	0.1	<0.1	<0.1
Veneridae sp.	1.0	0.1	<0.1	<0.1
Gastropoda				
Gastropoda sp.	2.1	1.4	1.3	1.7
Volutomitridae sp.	1.0	0.1	<0.1	<0.1
Pisces				
Unidentified sp.	22.7	2.2	26.5	59.1
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	97.9	9.2	21.8	201.1
Plastic fibres	3.1	0.3	0.2	<0.1

Cynoscion jamaicensis (n=33; E=0)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	3.0	0.9	0.3	0.3
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	0.0	0.0	0.0	0.0
Crustacea				
Unidentified sp.	12.1	20.4	3.2	65.2
Amphipoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Mysid-like decapoda sp.	18.2	36.1	2.3	83.3
Shrimp-like decapoda sp.	15.2	4.6	3.8	17.8
Shrimp-like decapoda sp. postlarva	0.0	0.0	0.0	0.0
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	6.1	2.8	4.2	11.7
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	6.1	1.9	4.5	8.4
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	0.0	0.0	0.0	0.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	30.3	11.1	52.6	584.5
Clupeiformes sp.	3.0	0.9	11.3	10.5
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	3.0	2.8	6.4	17.8
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	60.6	18.5	11.3	209.1
Plastic fibres	0.0	0.0	0.0	0.0

Cynoscion virescens (n=51; E=0)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	3.9	1.4	<0.1	0.1
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	2.0	0.7	<0.1	<0.1
Crustacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Amphipoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	21.6	9.8	7.8	76.6
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	25.5	12.6	6.7	84.9
Shrimp-like decapoda sp. postlarva	2.0	0.7	<0.1	<0.1
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	2.0	0.7	<0.1	<0.1
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	11.8	4.9	1.9	9.4
Nematopalaemon schmitti	3.9	4.2	3.8	15.9
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	2.0	1.4	0.7	1.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	51.0	28.0	43.7	1221.6
X. kroyeri postlarve	9.8	5.6	0.1	0.7
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	2.0	1.4	0.1	0.1
Squilla lijdingi	0.0	0.0	0.0	0.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	2.0	0.7	<0.1	<0.1
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	2.0	0.7	0.1	<0.1
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	25.5	11.9	5.1	60.5
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	2.0	0.7	1.0	0.7
Harengula jaguana	2.0	0.7	9.8	6.9
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	3.9	2.1	15.4	32.4
Others				
Digested debris	33.3	11.9	3.7	43.8
Plastic fibres	0.0	0.0	0.0	0.0

Dasyatis guttata (n=71; E=3)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	20.6	2.0	4.3	8.5
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	0.0	0.0	0.0	0.0
Crustacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Amphipoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	7.4	1.3	0.3	0.4
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	77.9	11.4	14.7	168.3
Shrimp-like decapoda sp. postlarva	0.0	0.0	0.0	0.0
Acetes americanus	1.5	0.1	0.1	<0.1
Axiidae sp.	25.0	6.4	2.9	18.8
Nephropidae sp.	7.4	0.5	1.8	0.9
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	7.4	0.5	0.9	0.5
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	23.5	1.4	2.0	2.9
Unidentified sp. larva	1.5	0.5	<0.1	<0.1
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	2.9	0.2	0.7	0.1
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	2.9	0.1	2.4	0.3
Ogyrides sp.	80.9	69.4	16.4	1138.7
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	4.4	0.2	5.2	0.9
Penaeus sp. postlarva	2.9	0.2	<0.1	<0.1
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	4.4	0.3	5.1	1.4
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	1.5	0.3	0.1	<0.1
Stomatopoda				
Unidentified sp.	23.5	1.4	3.1	4.3
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	2.9	0.2	1.9	0.3
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	1.5	0.1	<0.1	<0.1
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	1.5	0.1	<0.1	<0.1
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	97.1	3.6	37.8	135.7
Plastic fibres	0.0	0.0	0.0	0.0

Gymnura micrura (n=65; E=17)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	0.0	0.0	0.0	0.0
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	0.0	0.0	0.0	0.0
Crustacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Amphipoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	4.2	3.3	0.3	1.0
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	4.2	6.7	0.2	1.4
Shrimp-like decapoda sp. postlarva	0.0	0.0	0.0	0.0
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	2.1	1.7	2.5	4.1
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	2.1	3.3	0.3	0.9
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	0.0	0.0	0.0	0.0
Ogyrides sp.	2.1	1.7	<0.1	<0.1
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	0.0	0.0	0.0	0.0
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	0.0	0.0	0.0	0.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	72.9	61.7	81.1	4998.6
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	2.1	1.7	9.9	16.5
Others				
Digested debris	25.0	20.0	5.7	114.6
Plastic fibres	0.0	0.0	0.0	0.0

Macrodon ancylodon (n=92; E=1)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	1.1	0.6	<0.1	<0.1
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	1.1	1.3	<0.1	<0.1
Crustacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Amphipoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	17.6	12.9	2.8	36.0
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	2.2	1.3	0.1	0.2
Shrimp-like decapoda sp. postlarva	2.2	2.6	0.1	0.2
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	1.1	0.6	<0.1	<0.1
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	4.4	2.6	0.8	2.0
Nematopalaemon schmitti	5.5	3.2	1.4	4.4
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	1.1	1.3	<0.1	<0.1
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	1.1	0.6	13.1	8.5
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	15.4	12.3	12.3	150.2
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	0.0	0.0	0.0	0.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	47.3	34.2	43.5	1488.0
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	2.2	1.3	9.3	12.0
Engraulidae sp.	3.3	2.6	3.0	7.8
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	1.1	0.6	6.3	4.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	2.2	1.3	3.9	5.0
Others				
Digested debris	35.2	20.6	3.5	71.9
Plastic fibres	0.0	0.0	0.0	0.0

Nebris microps (n=66; E=1)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	0.0	0.0	0.0	0.0
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	4.6	1.6	<0.1	<0.1
Crustacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Amphipoda				
Unidentified sp.	1.5	0.4	<0.1	<0.1
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	16.9	7.9	6.1	48.2
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	24.6	16.6	5.1	84.4
Shrimp-like decapoda sp. postlarva	4.6	1.2	0.1	0.1
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	1.5	0.4	0.1	<0.1
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	12.3	4.0	7.2	28.3
Nematopalaemon schmitti	3.1	1.6	4.7	7.5
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	0.0	0.0	0.0	0.0

Species	%FO	%N	%G	Q
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	46.2	17.8	58.8	1046.2
X. kroyeri postlarve	23.1	16.6	1.7	28.5
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	0.0	0.0	0.0	0.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	27.7	7.5	3.3	24.5
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	1.5	0.4	0.8	0.3
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	93.8	24.1	12.1	291.5
Plastic fibres	0.0	0.0	0.0	0.0

Paralonchurus brasiliensis (n=63; E=3)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	68.3	55.6	35.9	1997.0
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	3.3	2.7	8.3	22.5
Platyhelminthes				
Platyhelminthes sp.	3.3	0.9	<0.1	<0.1
Crustacea				
Unidentified sp.	1.7	0.4	<0.1	<0.1
Amphipoda				
Unidentified sp.	10.0	4.5	0.3	1.3
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	16.7	5.4	1.8	9.4
Shrimp-like decapoda sp. postlarva	0.0	0.0	0.0	0.0
Acetes americanus	1.7	0.4	0.1	<0.1
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	1.7	0.4	0.3	0.1
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	3.3	0.9	1.2	1.1
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	0.0	0.0	0.0	0.0
Ogyrides sp.	3.3	0.9	0.6	0.6
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	3.3	0.9	8.4	7.5
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	1.7	0.4	<0.1	<0.1
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	0.0	0.0	0.0	0.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	1.7	0.4	1.8	0.8
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	3.3	1.3	7.4	9.9
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	91.7	24.7	33.8	833.9
Plastic fibres	0.0	0.0	0.0	0.0

Prionotus punctatus (n=67; E=4)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	4.8	0.9	0.1	0.1
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	38.1	11.7	0.9	10.7
Crustacea				
Unidentified sp.	1.6	1.5	0.1	0.1
Amphipoda				
Unidentified sp.	7.9	2.4	<0.1	0.1
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	1.6	0.6	<0.1	<0.1
Decapoda				
Unidentified sp.	3.2	0.6	0.4	0.2
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	36.5	27.6	16.1	445.1
Shrimp-like decapoda sp. postlarva	4.8	1.2	0.2	0.3
Acetes americanus	1.6	1.2	0.2	0.3
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	1.6	0.6	0.9	0.6
Solenocera sp.	1.6	0.6	1.0	0.6
Anomura				
Unidentified sp.	1.6	0.3	<0.1	<0.1
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	1.6	0.3	0.1	<0.1
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	4.8	1.5	1.9	2.8
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	4.8	0.9	1.2	1.1
Callinectes sp.	1.6	0.3	2.0	0.6
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	4.8	1.5	10.3	15.5
Hepatus pudibundus	1.6	0.3	2.0	0.6
Leiolambrus nitidus	1.6	0.6	0.2	0.1
Portunidae sp.	9.5	2.7	2.8	7.5
Portunus gibbesii	3.2	0.9	8.8	7.9
Portunus sp.	3.2	0.6	2.9	1.7
Caridae				
Exhippolysmata oplophoroides	1.6	0.3	0.2	<0.1
Nematopalaemon schmitti	1.6	0.3	0.2	0.1
Ogyrides sp.	11.1	5.4	3.0	16.1
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	9.5	3.0	1.2	3.5
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	1.6	1.2	6.5	7.8
Rimapenaeus sp.	6.3	3.0	6.4	19.3
Xiphopenaeus kroyeri	6.3	1.2	3.5	4.2
X. kroyeri postlarve	3.2	1.2	1.3	1.6
Mysida				
Unidentified sp.	1.6	0.9	<0.1	<0.1
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	4.8	1.2	1.2	1.4
Squilla lijdingi	4.8	0.9	3.8	3.4
Squilla obtusa	4.8	0.9	3.2	2.9
Mollusca				
Bivalvia				
Unidentified sp.	6.3	1.2	0.1	0.1
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	1.6	0.3	0.2	0.1
Pisces				
Unidentified sp.	6.3	2.1	0.6	1.2
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	1.6	0.3	0.8	0.2
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	93.7	17.7	15.8	280.5
Plastic fibres	0.0	0.0	0.0	0.0

Stellifer microps (n=39; E=4)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	0.0	0.0	0.0	0.0
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	0.0	0.0	0.0	0.0
Crustacea				
Unidentified sp.	2.9	1.2	0.6	0.7
Amphipoda				
Unidentified sp.	5.7	2.4	0.1	0.2
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Mysid-like decapoda sp.	2.9	1.2	<0.1	<0.1
Shrimp-like decapoda sp.	20.0	11.8	3.6	41.9
Shrimp-like decapoda sp. postlarva	0.0	0.0	0.0	0.0
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	2.9	1.2	1.6	1.9
Brachyura				
Unidentified sp.	14.3	5.9	3.1	18.2
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	20.0	14.1	12.0	169.9
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	2.9	1.2	0.3	0.4
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	0.0	0.0	0.0	0.0
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	14.3	5.9	4.2	24.5
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	20.0	8.2	26.0	213.9
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	20.0	14.1	7.9	111.4
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	2.9	1.2	1.8	2.1
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	77.1	31.8	38.9	1235.5
Plastic fibres	0.0	0.0	0.0	0.0

Stellifer rastrifer (n=48; E=1)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	2.1	0.4	<0.1	<0.1
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	0.0	0.0	0.0	0.0
Crustacea				
Unidentified sp.	6.4	1.1	<0.1	<0.1
Amphipoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	2.1	0.4	<0.1	<0.1
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	29.8	6.5	5.6	36.3
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp. postlarva	19.1	55.9	0.7	40.9
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	0.0	0.0	0.0	0.0
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	14.9	3.1	9.1	27.9
Nematopalaemon schmitti	6.4	1.9	6.7	12.8
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	8.5	2.3	0.1	0.2
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	6.4	1.9	1.2	2.2
X. kroyeri postlarve	10.6	4.2	2.8	11.8
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	2.1	0.4	2.6	1.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	46.8	9.2	69.3	637.2
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	2.1	0.4	0.4	0.2
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	66.0	11.9	1.4	17.1
Plastic fibres	2.1	0.4	<0.1	<0.1

Symphurus plagusia (n=32; E=1)

Species	%FO	%N	%G	Q
Polychaeta				
Unidentified sp.	9.7	8.1	3.6	28.9
Aonides sp.	0.0	0.0	0.0	0.0
Cirratulidae sp.	0.0	0.0	0.0	0.0
Platyhelminthes				
Platyhelminthes sp.	0.0	0.0	0.0	0.0
Crustacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Amphipoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Caprellidae sp.	0.0	0.0	0.0	0.0
Copepoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Cumacea				
Unidentified sp.	0.0	0.0	0.0	0.0
Decapoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Mysid-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp.	0.0	0.0	0.0	0.0
Shrimp-like decapoda sp. postlarva	0.0	0.0	0.0	0.0
Acetes americanus	0.0	0.0	0.0	0.0
Axiidae sp.	0.0	0.0	0.0	0.0
Nephropidae sp.	0.0	0.0	0.0	0.0
Sicyonia sp.	3.2	2.7	1.7	4.7
Solenocera sp.	0.0	0.0	0.0	0.0
Anomura				
Unidentified sp.	0.0	0.0	0.0	0.0
Clibanarius foresti	0.0	0.0	0.0	0.0
Diogenidae sp.	0.0	0.0	0.0	0.0
Porcellanidae sp.	0.0	0.0	0.0	0.0
Brachyura				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Calappa sp.	0.0	0.0	0.0	0.0
Calappidae sp.	0.0	0.0	0.0	0.0
Callinectes sp.	0.0	0.0	0.0	0.0
Dromiidae sp.	0.0	0.0	0.0	0.0
Hepatus gronovii	0.0	0.0	0.0	0.0
Hepatus pudibundus	0.0	0.0	0.0	0.0
Leiolambrus nitidus	0.0	0.0	0.0	0.0
Portunidae sp.	0.0	0.0	0.0	0.0
Portunus gibbesii	0.0	0.0	0.0	0.0
Portunus sp.	0.0	0.0	0.0	0.0
Caridae				
Exhippolysmata oplophoroides	0.0	0.0	0.0	0.0
Nematopalaemon schmitti	0.0	0.0	0.0	0.0
Ogyrides sp.	0.0	0.0	0.0	0.0
Palaemonidae sp.	0.0	0.0	0.0	0.0
Crustacea				
Decapoda				
Penaeidae				
Penaeus sp.	0.0	0.0	0.0	0.0
Penaeus sp. postlarva	0.0	0.0	0.0	0.0
Penaeus brasiliensis	0.0	0.0	0.0	0.0
Penaeus subtilis	0.0	0.0	0.0	0.0
Rimapenaeus similis	0.0	0.0	0.0	0.0
Rimapenaeus sp.	0.0	0.0	0.0	0.0
Xiphopenaeus kroyeri	3.2	2.7	0.7	1.8
X. kroyeri postlarve	0.0	0.0	0.0	0.0
Mysida				
Unidentified sp.	0.0	0.0	0.0	0.0
Stomatopoda				
Unidentified sp.	0.0	0.0	0.0	0.0
Unidentified sp. larva	0.0	0.0	0.0	0.0
Squilla sp.	0.0	0.0	0.0	0.0
Squilla lijdingi	0.0	0.0	0.0	0.0
Squilla obtusa	0.0	0.0	0.0	0.0
Mollusca				
Bivalvia				
Unidentified sp.	0.0	0.0	0.0	0.0
Mactridae sp.	0.0	0.0	0.0	0.0
Nuculidae sp.	0.0	0.0	0.0	0.0
Pectinidae sp.	0.0	0.0	0.0	0.0
Veneridae sp.	0.0	0.0	0.0	0.0
Gastropoda				
Gastropoda sp.	0.0	0.0	0.0	0.0
Volutomitridae sp.	0.0	0.0	0.0	0.0
Pisces				
Unidentified sp.	3.2	2.7	0.4	1.0
Clupeiformes sp.	0.0	0.0	0.0	0.0
Amphiarius sp.	0.0	0.0	0.0	0.0
Harengula jaguana	0.0	0.0	0.0	0.0
Symphurus plagusia	0.0	0.0	0.0	0.0
Engraulidae				
Anchoviella lepidentostole	0.0	0.0	0.0	0.0
Engraulidae sp.	0.0	0.0	0.0	0.0
Sciaenidae				
Cynoscion jamaicensis	0.0	0.0	0.0	0.0
Macrodon ancylodon	0.0	0.0	0.0	0.0
Paralonchurus sp.	0.0	0.0	0.0	0.0
Stellifer rastifer	0.0	0.0	0.0	0.0
Others				
Digested debris	100.0	83.8	93.6	7845.1
Plastic fibres	0.0	0.0	0.0	0.0

ANNEX 5.2. **List of average (± SD, ‰) carbon and nitrogen stable isotope signatures of fish length-species (this study) and different life stages of *Xiphopenaeus kroyeri* (Willems et al, submitted a).**

Species Length class	$\delta^{13}C$			$\delta^{15}N$			n
Achirus achirus							
small	-13.9	±	0.1	11.8	±	0.0	3
Amphiarius rugispinis							
small	-14.7	±	0.1	12.7	±	0.0	3
large	-14.9	±	0.1	13.2	±	0.0	3
Cynoscion virescens							
small	-15.0	±	0.1	11.5	±	0.0	3
large	-15.0	±	0.1	11.9	±	0.0	3
extra large	-14.3	±	0.1	14.6	±	0.0	3
Dasyatis guttata							
small	-14.7	±	0.0	11.4	±	0.0	3
large	-14.7	±	0.1	11.4	±	0.0	3
extra large	-13.9	±	0.0	11.9	±	0.1	3
Gymnura micrura							
small	-13.6	±	0.0	14.5	±	0.0	3
large	-14.6	±	0.0	12.9	±	0.1	3
extra large	-14.1	±	0.1	13.3	±	0.0	3
Macrodon ancylodon							
small	-15.2	±	0.1	11.2	±	0.1	3
large	-15.2	±	0.0	13.8	±	0.1	3
Nebris microps							
small	-14.9	±	0.0	11.6	±	0.1	3
large	-14.6	±	0.0	13.6	±	0.1	3
Paralonchurus brasiliensis							
small	-15.1	±	0.1	13.0	±	0.0	3
large	-14.7	±	0.1	12.9	±	0.0	3
Prionotus punctatus							
small	-16.7	±	0.1	12.6	±	0.1	3
large	-16.4	±	0.1	12.6	±	0.0	3
Stellifer microps							
small	-15.3	±	0.1	12.2	±	0.1	3
Stellifer rastrifer							
small	-14.9	±	0.0	12.9	±	0.1	3
Symphurus plagusia							
small	-15.5	±	0.1	11.3	±	0.0	3
Cynoscion jamaicensis							
small	-15.3	±	0.0	12.7	±	0.1	3
Xiphopenaus kroyeri							
adult	-14.7	±	0.2	10.8	±	0.5	18
juvenile	-15.4	±	0.2	9.4	±	0.1	11

ANNEX 5.3. **PERMANOVA P-values (drawn from Monte-Carlo tests) from pairwise comparisons of C and N SI composition of different fish species in length classes *small* (group S), *large* (group L) and *extra large* (group XL).** ***AA=Achirus achirus, AR=Amphiarius rugispinis, CJ=Cynoscion jamaicensis, CV=Cynoscion virescens, DG=Dasyatis guttata, GM=Gymnura micrura, MA=Macrodon ancylodon, NM=Nebris microps, PB=Paralonchurus brasiliensis, PP=Prionotus punctatus, SM=Stellifer microps, SR=Stellifer rastrifer, SP=Symphurus plagiusa.***

	C	N		C	N
Groups S			**Groups S**		
PB, AR	0.005	0.0008	**(continued)**		
PB, CJ	0.0175	0.0093	MA, NM	0.0012	0.0057
PB, SM	0.0606	0.0001	MA, CV	0.0164	0.0031
PB, SR	0.0068	0.3158	MA, PP	0.0003	0.0001
PB, SP	0.0034	0.0001	MA, AA	0.0001	0.0001
PB, MA	0.1281	0.0001	MA, GM	0.0001	0.0001
PB, NM	0.0061	0.0001	MA, DG	0.0002	0.0056
PB, CV	0.0904	0.0001	NM, CV	0.2129	0.3282
PB, PP	0.0001	0.0033	NM, PP	0.0001	0.0002
PB, AA	0.0001	0.0002	NM, AA	0.0001	0.0062
PB, GM	0.0001	0.0001	NM, GM	0.0001	0.0001
PB, DG	0.0007	0.0001	NM, DG	0.001	0.0658
AR, CJ	0.0008	0.8982	CV, PP	0.0001	0.0001
AR, SM	0.0016	0.0003	CV, AA	0.0002	0.0009
AR, SR	0.0337	0.0084	CV, GM	0.0001	0.0001
AR, SP	0.0005	0.0001	CV, DG	0.0038	0.0864
AR, MA	0.0027	0.0001	PP, AA	0.0001	0.0002
AR, NM	0.0513	0.0001	PP, GM	0.0001	0.0001
AR, CV	0.0306	0.0001	PP, DG	0.0001	0.0001
AR, PP	0.0001	0.1828	AA, GM	0.0048	0.0001
AR, AA	0.0006	0.0001	AA, DG	0.0003	0.0004
AR, GM	0.0003	0.0001	GM, DG	0.0001	0.0001
AR, DG	0.4852	0.0001			
CJ, SM	0.8356	0.0035	**Groups L**		
CJ, SR	0.0001	0.0264	PB, AR	0.0343	0.0003
CJ, SP	0.0202	0.0001	PB, MA	0.0016	0.0001
CJ, MA	0.2064	0.0001	PB, NM	0.0914	0.0002
CJ, NM	0.0002	0.0002	PB, CV	0.0192	0.0001
CJ, CV	0.0041	0.0001	PB, PP	0.0001	0.0002
CJ, PP	0.0002	0.3392	PB, GM	0.1432	0.664
CJ, AA	0.0001	0.0003	PB, DG	0.9417	0.0001
CJ, GM	0.0001	0.0001	AR, MA	0.0077	0.0001
CJ, DG	0.0001	0.0003	AR, NM	0.0017	0.0005
SM, SR	0.0015	0.0006	AR, CV	0.7256	0.0001
SM, SP	0.0479	0.0002	AR, PP	0.0001	0.0001
SM, MA	0.4245	0.0001	AR, GM	0.0028	0.0003
SM, NM	0.0015	0.0004	AR, DG	0.0174	0.0001
SM, CV	0.0136	0.0004	MA, NM	0.0002	0.0202
SM, PP	0.0001	0.0066	MA, CV	0.006	0.0001
SM, AA	0.0001	0.0007	MA, PP	0.0001	0.0001
SM, GM	0.0001	0.0001	MA, GM	0.0001	0.0001
SM, DG	0.0004	0.0001	MA, DG	0.0006	0.0001
SR, SP	0.0006	0.0001	NM, CV	0.0009	0.0001
SR, MA	0.002	0.0001	NM, PP	0.0001	0.0001
SR, NM	0.4274	0.0001	NM, GM	0.2484	0.0001
SR, CV	0.2947	0.0001	NM, DG	0.0436	0.0001
SR, PP	0.0001	0.0089	CV, PP	0.0001	0.0002
SR, AA	0.0001	0.0003	CV, GM	0.0007	0.0001
SR, GM	0.0001	0.0001	CV, DG	0.0092	0.0004
SR, DG	0.0005	0.0001	PP, GM	0.0001	0.0015
SP, MA	0.0132	0.2598	PP, DG	0.0001	0.0001
SP, NM	0.0005	0.035	GM, DG	0.0721	0.0001
SP, CV	0.0017	0.0469			
SP, PP	0.0001	0.0003	**Groups XL**		
SP, AA	0.0001	0.002	CV, GM	0.1773	0.0001
SP, GM	0.0001	0.0001	CV, DG	0.0015	0.0001
SP, DG	0.0001	0.1574	GM, DG	0.0109	0.0001

ANNEX 6.1. The parameters *a* and *b* used to calculate fish weight (W) from the total length (L) according to the formula W = a * Lb. Average values of the parameters were used based on the studies available on FishBase (Froese and Pauly (Eds.), 2015), at species or, if unavailable, genus level.

Species	a	b	N studies	Species/genus
Achirus achirus	0.0168	2.995	1	species
Anchoa spinifer	0.00396	3.18	1	species
Anchoviella lepidentostole	0.0046	3.2	4	species
Aspistor quadriscutis	0.0105	2.9	2	genus
Bagre bagre	0.0059	3.02	2	species
Batrachoides surinamensis	0.0071	3.21	3	species
Caranx hippos	0.0447	2.77	2	species
Cathorops phrygiatus	0.0105	2.96	2	genus
Cathorops rugispinis	0.0105	2.96	2	species
Centropomus ensiferus	0.0039	3.298	1	species
Chaetodipterus faber	0.0372	2.89	7	species
Chilomycterus antillarum	0.02	3	2	genus
Colomesus psittacus	0.0316	2.82	4	species
Ctenosciaena gracilicirrhus	0.0132	3.01	5	species
Cynoponticus savanna	0.004	2.686	1	genus
Cynoscion jamaicensis	0.0069	3.13	10	species
Cynoscion virescens	0.0047	3.08	2	species
Dactylopterus volitans	0.0141	2.92	6	species
Dasyatis geijskesi	0.0739	2.81	2	genus
Dasyatis guttata	0.0739	2.81	2	genus
Diplectrum sp.	0.0079	3.16	10	genus
Gymnothorax ocellatus	0.00027	3.446	1	species
Gymnura micrura	0.0174	2.98	2	genus
Haemulon boschmae	0.0191	2.97	47	genus
Harengula jaguana	0.0087	3.33	4	species
Harengula sp.	0.0081	3.2	14	genus
Larimus breviceps	0.0095	3.12	5	species
Lonchurus lanceolatus	0.0036	3.26	13	genus
Macrodon ancylodon	0.0037	3.25	11	species
Menticirrhus americanus	0.0047	3.21	9	species
Micropogonias furnieri	0.011	3.01	23	species
Mustelus higmani	0.00652	3	1	genus
Narcine brasiliensis	0.0129	2.87	2	species
Nebris microps	0.0078	3.08	3	species
Notarius grandicassis	0.0123	2.89	2	genus
Odontognathus mucronatus	0.0035	3.02	2	species
Ogcocephalus sp.	0.0154	3.063	1	genus
Orthopristis ruber	0.0138	2.96	7	species
Paralonchurus brasiliensis	0.0028	3.37	3	species
Paralonchurus elegans	0.0028	3.37	3	genus
Peprilus paru	0.0257	2.87	8	species
Plagioscion auratus	0.012	3.05	6	genus
polydactylus oligodon	0.0112	3	1	species
Prionotus punctatus	0.0095	3.05	9	species
Rhinobatos percellens	0.0059	2.89	2	species
Saurida caribbaea	0.00719	2.844	1	species
Selene brownii	0.048	2.83	1	species
Selene vomer	0.0178	2.82	7	species
Sphoeroides testudineus	0.0224	2.9	13	species
Stellifer microps	0.0058	3.32	2	species
Stellifer rastrifer	0.0074	3.16	9	species
Symphurus plagusia	0.0091	2.98	2	species
Trichiurus lepturus	0.0005	3.15	19	species
Urotrygon microphthalmum	0.006	3.04	1	genus

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Tomas

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The Ecosystem Approach to Fisheries (EAF) is widely regarded as the best way to manage our living marine resources. While traditional fisheries management focuses on the populations of the target species, an EAF recognizes the complexity of ecosystems in which fisheries operate. Crucial aspects of an EAF are therefore (1) trophic relations between target species, their prey and predators, (2) indirect interactions between fleets - through trophic links and bycatch - and (3) the impact of fishing on marine habitats and species communities. Ignoring these elements in fisheries management lies at the core of different environmental and socio-economic problems, particularly in tropical shrimp fisheries. Triggered by a negative public perception and increasing consumer demand for sustainable products, the fishery for seabob shrimp in Suriname launched a sustainability initiative, resulting in certification by the Marine Stewardship Council (MSC). This eco-label, however, was not an endpoint, but formed the basis for further improvements and was the direct motivation for this doctoral study.

In cooperation with the local fisheries administration, the fishing industry, NGOs and the local university, research was conducted on the coastal ecosystem in Suriname, until recently virtually a blind spot for marine biologists. First, we investigated the spatio-temporal distribution of fish and invertebrates in the coastal waters. A second important element was the characterization of the role of seabob shrimp in the marine food web. Thirdly, this study focused on assessing the impact of seabob fisheries on the coastal ecosystem, by examining the composition of commercial catches. The scientific results were translated into recommendations to further support an ecosystem approach to the management of the Suriname seabob fishery. This thesis shows that fisheries can be sustainably managed, even those targeting tropical shrimp. Eco-labelling, participatory management and research can play a crucial role in this process.

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